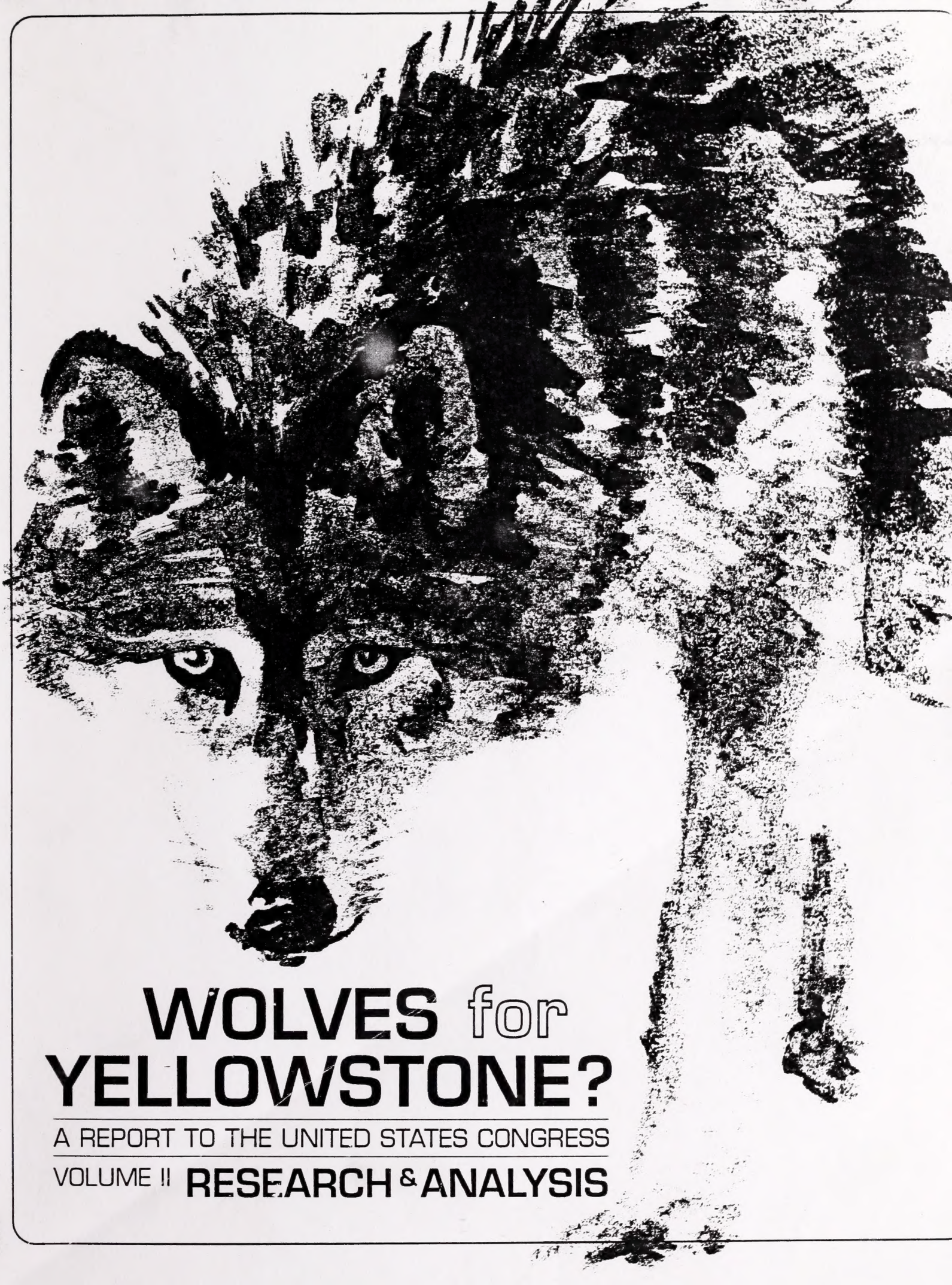

WOLVES for YELLOWSTONE?

A REPORT TO THE UNITED STATES CONGRESS

VOLUME II **RESEARCH & ANALYSIS**

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WOLVES FOR YELLOWSTONE?

A Report to the United States Congress

Volume II Research and Analysis

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WOLVES FOR YELLOWSTONE?
A REPORT TO THE UNITED STATES CONGRESS
VOLUME II RESEARCH AND ANALYSIS

Prepared by

Yellowstone National Park

U.S. Fish and Wildlife Service

University of Wyoming

University of Idaho

Interagency Grizzly Bear Study Team

University of Minnesota Cooperative Park Studies Unit

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INTRODUCTION

Proposals from concerned citizens and organized groups prompted Congress in 1988 to investigate a proposed wolf restoration to Yellowstone National Park. The findings of related studies are detailed in this report. The issue of wolf recovery is controversial; the roots of the controversy reach back into our nation's history. Our European forebears began to make North America safe for domestic animals soon after the first colony had landed, and we had purposely eliminated wolves nationwide by the 1940s.

What do we need to know before we restore wolves to Yellowstone? Is it a biologically viable idea? The next few paragraphs are an attempt to answer some of the questions. The report that follows responds to questions posed by Congress in 1988.

Yellowstone National Park was established in 1872, but slaughter of its big game animals continued through the 1880s; thousands of elk, bighorn sheep, deer, antelope, moose, and bison were killed for their tongues and hides, and their carcasses strychnine-poisoned to kill coyotes, wolves, or wolverines. In 1886 the U.S. Army was assigned to guard Yellowstone and protect its features and wildlife. The Army was pressured to control predators, but in 1897 observers predicted range damage by gophers if coyotes were exterminated. Meanwhile in Montana alone, 80,730 wolves were killed for bounty from 1883 to 1918.

In 1914 the U.S. Congress passed a law to eliminate predatory animals from all public lands, including national parks. By 1922 some people questioned destruction of wolves in the park, but from 1914 to 1926, 136 wolves were killed in Yellowstone. Pack activity had been eliminated and has not been confirmed since the 1930s. About the same time, 121 mountain lions and 4,352 coyotes were also killed in Yellowstone.

By 1933 National Park Service policy stated, "no native predator shall be destroyed on account of its normal utilization of any other park animal," and "no management measure or other interference with biotic relationships shall be undertaken prior to a properly conducted investigation." Yet predator control continued in Yellowstone through the winter of 1934-1935, and war was waged against predators on all the park boundaries with cyanide "coyote getters" and Compound 1080 baits until stopped by Executive Order in the early 1970s.

Adolph Murie wrote the first objective ecological treatise on wolves, The Wolves of Mount McKinley, in 1944. Since that time, dozens of scientists throughout the northern hemisphere have added to our knowledge of wolves. Many of those scientists studied wolves in national parks or similar

reserves: Denali, as Mount McKinley was renamed in 1980; Isle Royale; Alberta's Jasper National Park; Manitoba's Riding Mountain; Ontario's Algonquin Provincial Park; and nature reserves of the Soviet Union.

A quarter of a century after Murie's wolf study was published, The Endangered Species Act of 1973 (ESA) recognized that some fish, wildlife, and plants were endangered by economic growth and development. The ESA provided for conserving endangered and threatened species and the ecosystems they depend upon, in cooperation with other nations. The ESA stated "[it is] the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species."

The gray wolf is listed as endangered in the 48 conterminous states except Minnesota, where it is listed as threatened. Fulfilling the agency's lead responsibility under ESA, the U.S. Fish and Wildlife Service produced a Northern Rocky Mountain Wolf Recovery Plan in 1980 and a revision approved in 1987. The plan offered strategies for conserving gray wolves in the northern Rocky Mountains. Three areas were considered appropriate for recovery of gray wolves: northwest Montana, central Idaho, and the greater Yellowstone area. In the first two areas, the plan projected wolves would naturally colonize. In fact, a small population of wolves has colonized an area in northwest Montana in the last decade, and central Idaho has persistent reports of wolves.

Due to Yellowstone's geographic isolation from areas with established wolf populations, the recovery plan proposed translocating wolves to the Yellowstone area. That proposal raised a number of questions and concerns about the potential effects of restoring wolves to Yellowstone.

In 1988 the Senate-House Interior Appropriations Conference Committee appropriated $200,000 for the National Park Service and the U.S. Fish and Wildlife Service to address five issues related to restoring wolves to Yellowstone. They wrote:

> The managers agree that the return of the wolf to Yellowstone NP is desirable. There are a number of concerns about the reintroduction and $200,000 has been included to study questions which have been raised. The managers believe the studies should address, but not be limited to the following:
>
> 1. The issue of whether wolves would or would not be controlled either within or without the Park;
> 2. How a reintroduced population of wolves may affect the prey base in Yellowstone NP and big game hunting in areas surrounding the park;
> 3. Would a reintroduced population of wolves harm or benefit grizzly bears in the vicinity of the park;
> 4. Clarification and delineation of wolf management zone boundaries for reintroduction; and
> 5. An experienced wolf coordinator with the FWS will oversee the program in full cooperation with the NPS.

Dr. Steven H. Fritts has been appointed as Rocky Mountain Wolf Coordinator, Montana-Wyoming Field Office, U.S. Fish and Wildlife Service, meeting the requirement of Item 5.

To answer the four questions, the National Park Service and the U.S. Fish and Wildlife Service employed three diverse approaches to gather the information: 1) extensive literature surveys; 2) consultation and compilation of the opinions of 15 experts on North American wolves, bears, and ungulates through a process known as the Delphi technique, and consultation with experts on Eurasian wolves, bears, and ungulates; and 3) development of three computer simulations by predator/prey dynamics modelers at two universities. Wildlife agencies of Idaho, Montana, and Wyoming furnished data for several of the ten resulting studies in this report.

The conclusions and opinions expressed in the studies are those of the authors and Delphi panelists. They were asked to evaluate the potential effects of wolf recovery in Yellowstone in relation to the four questions posed by Congress. They were not asked to evaluate the desirability of wolf recovery in Yellowstone.

The studies should be considered progress reports; the authors will want to read what others have written, and they may want to modify their conclusions based on more complete information. For instance, not all the data on Yellowstone area wolf prey numbers, ungulate ranges and harvests were available to the Delphi panelists (15 wolf/prey experts) when they offered their opinions on questions posed to them.

Questions remain and funding to study them has been appropriated for 1990. Some questions can never be answered definitively unless wolves are experimentally restored and studied in Yellowstone.

SECTION 1

Control and Management of Wolves

MANAGEMENT OF WOLVES INSIDE AND OUTSIDE YELLOWSTONE NATIONAL PARK AND POSSIBILITIES FOR WOLF WOLF MANAGEMENT ZONES IN THE GREATER YELLOWSTONE AREA

Steven H. Fritts
U.S. Fish and Wildlife Service
Federal Building, U.S. Courthouse
301 South Park
Helena, MT 59626

MANAGEMENT OF WOLVES INSIDE AND OUTSIDE YELLOWSTONE NATIONAL PARK AND POSSIBILITIES FOR WOLF MANAGEMENT ZONES IN THE GREATER YELLOWSTONE AREA

Steven H. Fritts, U.S. Fish and Wildlife Service, Federal Building, U.S. Courthouse, 301 South Park, Helena, MT 59626

EXECUTIVE SUMMARY

1. The need for control of wolves (Canis lupus) within Yellowstone National Park is expected to be negligible and limited mainly to occasional control of nuisance animals.

2. Any control is likely to be controversial. Some control will be needed outside the park to address occasional depredations on livestock and, possibly, to control excessive predation on ungulates.

3. The situation appears to be suited for reintroduction under Section 10(j) of the Endangered Species Act as a nonessential experimental population.

4. If a reintroduced population was classified as experimental and nonessential per Section 10(j) of the Endangered Species Act, federal agencies would only have to confer informally with the U.S. Fish and Wildlife Service (FWS) on activities that might jeopardize the species (except in national parks and national wildlife refuges). A jeopardy ruling by the FWS would not prohibit the federal agency from committing resources to the proposed activity. Therefore, land-use restrictions are not expected to be major issues.

5. Discussions with the Office of the Solicitor, Department of Interior, and review of the legislative history of Section 10(j) of the Endangered Species Act reveal that Congress intended broad flexibility for controlling experimental populations in order to make more reintroductions possible. The full extent of control possible under Section 10(j) has not been tested.

6. The court case of Sierra Club et al. vs. Clark et al. (1985) in Minnesota did not pertain to experimental populations and therefore will not affect the management of wolves in the greater Yellowstone area (GYA).

7. The experimental population designation was recently used to successfully reintroduce the red wolf (Canis rufus) to the wild; an account of that case with discussion of control methods used is provided.

8. Presence of wolves in Yellowstone National Park would not preclude usual recreational activities in the park or surrounding lands. Wolves would not be a significant threat to human safety.

9. If wolves were to colonize the GYA (including Yellowstone National Park) on their own, the opportunity for management flexibility via experimental population designation would be lost, and wolves would receive the full protection of the Endangered Species Act.

10. The purpose of this report was not to make specific recommendations about wolf control and management zones for wolves in the GYA but to identify and give advantages and disadvantages of some of the numerous options available. Various scenarios are discussed, ranging from intensive control with public involvement to no control or minor control conducted by state or federal officials. In general, less control means increased potential for conflicts but reduced risk to the wolf population, reduced time to recovery (10 breeding pairs) and delisting, and greater probability of reaching recovery level. Conversely, more control means fewer conflicts but increased risk to the wolf population, more time required to reach recovery and delisting, and reduced chance of achieving recovery level. The opportunity exists to craft management that will both allow wolf recovery and address the potential conflicts in the GYA.

11. An integral question to the management (and therefore, to establishment of management zones) of wolves in the GYA is how much area wolves would require for a secure population to be established. No research, short of placing wolves in the park, can answer that question without conjecture.

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MANAGEMENT OF WOLVES INSIDE AND OUTSIDE YELLOWSTONE NATIONAL PARK AND POSSIBILITIES FOR WOLF MANAGEMENT ZONES IN THE GREATER YELLOWSTONE AREA

Steven H. Fritts, U.S. Fish and Wildlife Service, Federal Building, U.S. Courthouse, 301 South Park, Helena, MT 59626

ABSTRACT: While the need to control wolves (Canis lupus) inside Yellowstone National Park is expected to be negligible, some management/control of wolves outside the park will be needed to alleviate depredations on livestock and possibly to reduce impacts on ungulate species in instances where excessive predation conflicts with state ungulate management objectives. There appears to be no reason why wolves could not be reintroduced to Yellowstone National Park or other portions of the Greater Yellowstone Area (GYA) as a nonessential experimental population under Section 10(j) of the Endangered Species Act (ESA). Designation of an experimental population involves preparation and publication in the Federal Register of a rule detailing the geographic location of the experimental population and identifying procedures to be used in its management. Section 10(j) was intended by Congress to address situations like the reintroduction of wolves to Yellowstone in which local opposition to a reintroduction exists and management flexibility is needed. Legal authority exists under Section 10(j) to authorize control of wolves although the full extent of control possible is not clear at this time. Wolf management (control) and management zones should provide for the protection of wolves over an area of sufficient size to allow the population to reach recovery level and maintain itself over a significant period, while keeping conflicts at a minimal level. Theoretically, control options could range from allowing the public to kill wolves on public and private lands up to the park boundary to no control anywhere in the GYA or whatever area is defined as containing the experimental population. Because of the migratory movements of most prey in the GYA and the uncertainty about how wolves will utilize that prey, it is extremely difficult to assess in advance the amount of area that will be necessary for the wolf population to attain recovery level. Any specific control recommendations are deferred at this time except to suggest that it would be desirable for the states of Idaho, Montana, and Wyoming to participate fully in wolf management via development of a conservation plan(s) to allow some control to manage conflict while ensuring the long-term conservation of the species. The experimental population designation may contain the flexibility to allow the public to control wolves on private land in response to depredations on livestock (some additional conditions apply). This concession would go far in achieving support for a reintroduction within the GYA, while having little impact on the conservation of the wolf. Public lands within and surrounding Yellowstone are of sufficient size and support the prey biomass to sustain a sizable wolf population without the need for protection on private land too. Control of wolves in the GYA can be expected to generate strong and widespread public interest, and some resistance can be expected. If relocation of problem wolves is planned, involved agencies would need to identify and prioritize potential release sites and obtain advance authority from involved land management agencies to release wolves captured in control actions. Using different management strategies in different areas (zones) provides a reasonable means of balancing the needs of the wolf with socioeconomic concerns in the area. The opportunity exists to craft a wolf management/control zone system that will both ensure the recovery of the wolf in the GYA and yet hold effects on other activities to a minimum level.

INTRODUCTION AND BACKGROUND

The gray wolf (Canis lupus) is different things to different people. To many the animal is a symbol, to some a symbol of wilderness, to others a symbol of evil. Even though in recent years much objective information has been disseminated about this animal, it is very difficult for humans to see this species strictly in biological terms (Lopez 1978, Fogleman 1989). Something about the wolf stirs strong feelings in humans -- feelings far out of proportion to the impact wolves will have on their lives. When humans begin to discuss wolves, total objectivity is very difficult to maintain. We would be wise to keep these things in mind throughout all evaluations of the feasibility of returning the wolf to Yellowstone.

There currently is a great deal of interest in restoring wolves to Yellowstone National Park. The Northern Rocky Mountain Wolf Recovery Plan identified the park as one of three recovery areas for the wolf in the Northern Rockies and recommended reintroduction of the wolf there because natural recolonization appeared unlikely (U.S. Fish and Wildlife Service 1987). The return of the wolf to the Yellowstone ecosystem would to many people be the most exciting and significant conservation accomplishment of the late twentieth century. Some not only believe that the wolf should be restored to Yellowstone but that the effort to do so is progressing far too slowly. Congressman Wayne Owens (Utah) has introduced H.R. 2786 which would initiate an Environmental Impact Statement (EIS) for restoring the wolf to Yellowstone as an experimental population and establish a timetable for selecting and implementing the preferred alternative (assumed by the sponsors to be reintroduction). Senator James McClure (Idaho) has circulated a proposal for the legislative restoration of wolves in Yellowstone National Park and portions of central Idaho apart from the Endangered Species Act (ESA) and related processes (Haywood 1989). Other members of Congress have expressed strong opposition to wolf reintroduction In 1988, the Senate-House Interior Appropriations Conference Committee raised the issue of a reintroduction to Yellowstone and appropriated $200,000 to be used by the National Park Service (NPS) and the U.S. Fish and Wildlife Service (FWS) to study five questions/issues related to wolf restoration in the Greater Yellowstone Area (GYA):

> The managers agree that the return of the wolf to Yellowstone NP is desirable. There are a number of concerns about the reintroduction and $200,000 has been included to study questions which have been raised. The managers believe the studies should address but not be limited to the following:
>
> 1. The issue of whether wolves would or would not be controlled either within or without the Park;
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> 2. How a reintroduced population of wolves may affect the prey base in Yellowstone NP and big game hunting in areas surrounding the park;
>
> 3. Would a reintroduced population of wolves harm or benefit grizzly bears in the vicinity of the park;

4. Clarification and delineation of wolf management zone boundaries for reintroduction; and

5. An experienced wolf coordinator with the FWS will oversee the program in full cooperation with the NPS (H.R. Rept. No. 862, 100th Cong., 2nd Sess. 14-15 (1988).

The issues of wolf control and wolf management zones (items 1 and 4, respectively) are closely intertwined and have been treated concurrently in section 1 of this report completed by the FWS. Items 2 and 3 were addressed by the NPS and university contractors. Results from these studies comprise sections 2, 3, and 4 of the document. Item 5 was fulfilled when an "experienced wolf coordinator" entered on duty in March 1989.

Definitions

Various terms used in this report may require clarification; therefore, the following definitions are provided:

Control is defined as any nonlethal or lethal intentional taking (definition below) directed at specific individuals or populations and conducted by government agents, their designees, or private citizens. Problem wolves (those confirmed to be involved in depredations on lawfully present domestic animals) taken in control activities could be relocated to remote areas on federal lands in the GYA or placed in captivity.

Experimental population means any population (including any offspring arising solely therefrom) authorized by the Secretary of the Interior for release outside the current range of the species only when, and at such times as, the population is separate geographically from nonexperimental populations of the same species. The term applies to populations derived from endangered or threatened species for which the Secretary has determined that such a release will further the conservation of that species (Sec. 10(j)).

Greater Yellowstone Area as defined in The Greater Yellowstone Area: An Aggregation of National Park and National Forest Management Plans (1987) encompasses approximately 11.7 million acres and is comprised of two national parks and six national forests. In addition, state lands, national wildlife refuges, unreserved public domain, unreserved public lands (Bureau of Land Management) and other lands are included.

In keeping with the idea of an ecosystem, the boundaries are defined by the "resources and the area they cover." The governmental units within the Greater Yellowstone Area include:

- Madison Ranger District of the Beaverhead National Forest
- Western portion of the Beartooth Ranger District of the Custer National Forest

- Gallatin National Forest south of Interstate 90
- Shoshone National Forest, except for the Lander Ranger District
- Bridger-Teton National Forest except for the Kemmerer Ranger District and the southern portions of the Big Piney and Pinedale Ranger Districts
- Targhee National Forest, except for the Dubois Ranger District
- The portion of the Caribou National Forest administered by the Targhee
- Yellowstone National Park
- Grand Teton National Park, including the John D. Rockefeller Jr. Memorial Parkway

Red Rock Lakes and the National Elk Wildlife Refuges are included in most resources concerning wildlife. Other information readily available was included for other federal and state managed lands and some privately owned lands (Greater Yellowstone Coordinating Committee 1987).

Management zones would merely be distinct geographic areas where wolves would be managed differently based on, for example, biological suitability of the habitat, the need for protection, and/or socioeconomic concerns.

Taking, as used in this report, is consistent with the definition in the Endangered Species Act, i.e., "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct" (Sec. 3(19)).

Nuisance Wolf refers to a wolf that causes concern for the safety of humans and/or pets by its repeated appearance, unusual behavior, and demonstration of any evidence of aggression toward or loss of fear of humans.

Background and Perspective

Wherever wolf reintroduction may be contemplated in the United States, major debate can be expected over the issue of control. Every successful effort to reestablish wolves will eventually require a management program (Mech 1979, Vales and Peek 1990). Accordingly, some control of wolves would eventually be necessary in the GYA. Some control will probably be accepted by almost all interest groups involved; the disagreement will be over what circumstances warrant control and how much is needed. Some individuals and conservation/wolf-advocate groups seem inherently to oppose most control of wolves (especially at the hands of the public) even when the impact on the wolf population may be negligible. On the other hand, those who feel their economic interests will be threatened oppose reintroduction (Bath 1987b:4, Miniclier 1987, M. Axsom pers. comm.) and may assert that a high level of wolf control would be necessary to minimize the effect of wolves on livestock and big game (Bath 1987c).

At this point, we do not know if the primary recovery area would be defined as Yellowstone National Park (where the potential for conflicts will be minor) or as all or portions of the six surrounding national forests and other GYA lands. Regardless or whether the park is so designated, if a population can be established, wolves will eventually travel outside park boundaries onto national forest and wilderness lands and beyond. There they would have the potential of depredating on cattle, sheep, and horses on grazing allotments and could affect game herds, some of which may already be harvested at or near maximum sustained yield (Mack et al. 1990, Vales and Peek 1990). Wolves will also travel onto private land near the park boundary, further increasing the potential for conflicts with livestock. Moreover, some wolves inside and outside the park will eventually engage in nuisance behavior.

Wolf management zones could be defined for the GYA according to different management needs in different areas (Mech 1979). It is reasonable to provide a reestablishing wolf population with maximum protection in a core area where the environment is suitable and the potential for conflict is small, while providing lesser protection with increasing distance away from such an area where the survival of individual wolves is not as critical to attaining recovery levels. There may be biological reasons why the wolf can and should be managed differently outside than inside the park. If for no other reason, wolf management inside and outside of Yellowstone can be expected to differ because of differing management agency mandates. Without actually observing wolf pack behavior in the Yellowstone area, it is not possible to predict exactly how much protection the wolf would require outside park boundaries for a viable population to develop and be maintained within the GYA.

The following discussion addresses the legal basis for control and then discusses wolf control inside and outside Yellowstone National Park. The matter of control within the park is relatively straightforward. The nature and extent of control outside the park depends largely on whether wolves can be designated as an "experimental population" and how much flexibility for control is possible under that designation. Four important control-related questions are central to the potential reestablishment of wolves in Yellowstone National Park and surrounding areas: 1) Would control be necessary and how much would be advisable? 2) Does the legal authority exist or can it be put in place to sanction control? 3) Under what conditions would control occur? and 4) Specifically, who would be authorized to take wolves under those conditions, and would state or federal authorities conduct or oversee the taking? A high degree of interest centers upon these questions, and the answers are pivotal in determining the level of public support that a restoration program in the GYA may expect locally and nationally. With such a diversity of views on the wolf and such a wide range of economic perspectives and value systems in the GYA, intense discussions of control measures are certain to occur during the planning phase for a reintroduction. The intensity of that discussion could even escalate after wolves are restored. A creative resolution of the control question will have to be made if wolf recovery in the Yellowstone area is to be acceptable to the diverse public interested in this issue.

As implied above, control cannot realistically be considered as only a biological issue. It is an intensely political issue as well. Control of

wolves appears to be unpopular with the national public, except in the case of directed control of specific wolves that have depredated livestock (Kellert 1985a). Public opinion surveys conducted in the Yellowstone area to date suggest that conservation groups and livestock-production groups have widely differing expectations about the impacts of wolves on livestock and game species (Bath 1987a,b,c); thus, they would have differing views on how much wolf control will be needed. Nonetheless, the park visitors generally support wolf recovery (McNaught 1987).

The public objected to efforts by state and provincial agencies to implement or liberalize some control programs in Alaska, Minnesota, and Canada; and some programs have been the subject of litigation. Two recent wolf control efforts conducted by the FWS in northwestern Montana (in response to livestock depredations) have been spotlighted by members of local and state news media and anticontrol sentiment has been especially strong. Because of the national prominence of Yellowstone Park and the intensity of public use there together with broad interest in the wolf, control efforts in the GYA will likely be covered by the national news media and come under immediate scrutiny by the American public. Finally, public opinion surveys of residents of Montana and Wyoming (discussed below) indicate disagreement on whether wolves should be reintroduced, and widely disparate views are held by interest groups (Bath 1987c, 1990). Only 21% of Wyoming residents surveyed (Bath 1987b:58) indicated that the wolf reintroduction issue was not important to them!

The opinion has frequently been expressed by residents of the GYA that no wolf control will occur there, despite the intent of government wildlife agencies, because of litigation from conservation groups. That skepticism, shared to some extent by state wildlife agencies, has helped fuel opposition to wolf reintroduction. Indeed, expressions of opposition and attempts to stop control efforts by individuals and groups located outside the Yellowstone area would not be surprising.

A 1985 decision by the U.S. Court of Appeals for the Eighth Circuit, in the case of Sierra Club et al. vs. William Clark et al. (hereafter referred to as Sierra Club vs. Clark) has been of concern to state wildlife officials because of the potential effect on the control and management of the Northern Rocky Mountain wolf. The states of Montana, Wyoming, and Idaho have maintained that the court's decision which prohibited public sport hunting of the "threatened" wolf in Minnesota would jeopardize the use of public hunting or trapping to control individual wolves that roam outside the "primary" or "core" Yellowstone recovery area. A major event relative to wolf control in the GYA came via the 1982 amendments to the Endangered Species Act of 1973 (specifically Sec 10(j)). The amendment added significantly to the Secretary of Interior's flexibility in developing regulations for reintroduced populations. However, that flexibility has not been used extensively, the details of experimental population designation are not well known, and the full extent of the Secretary's authority to allow the taking of members of experimental populations has not been explored.

With the above information as background, we approach the subject of wolf control in Yellowstone National Park and the surrounding area. The following

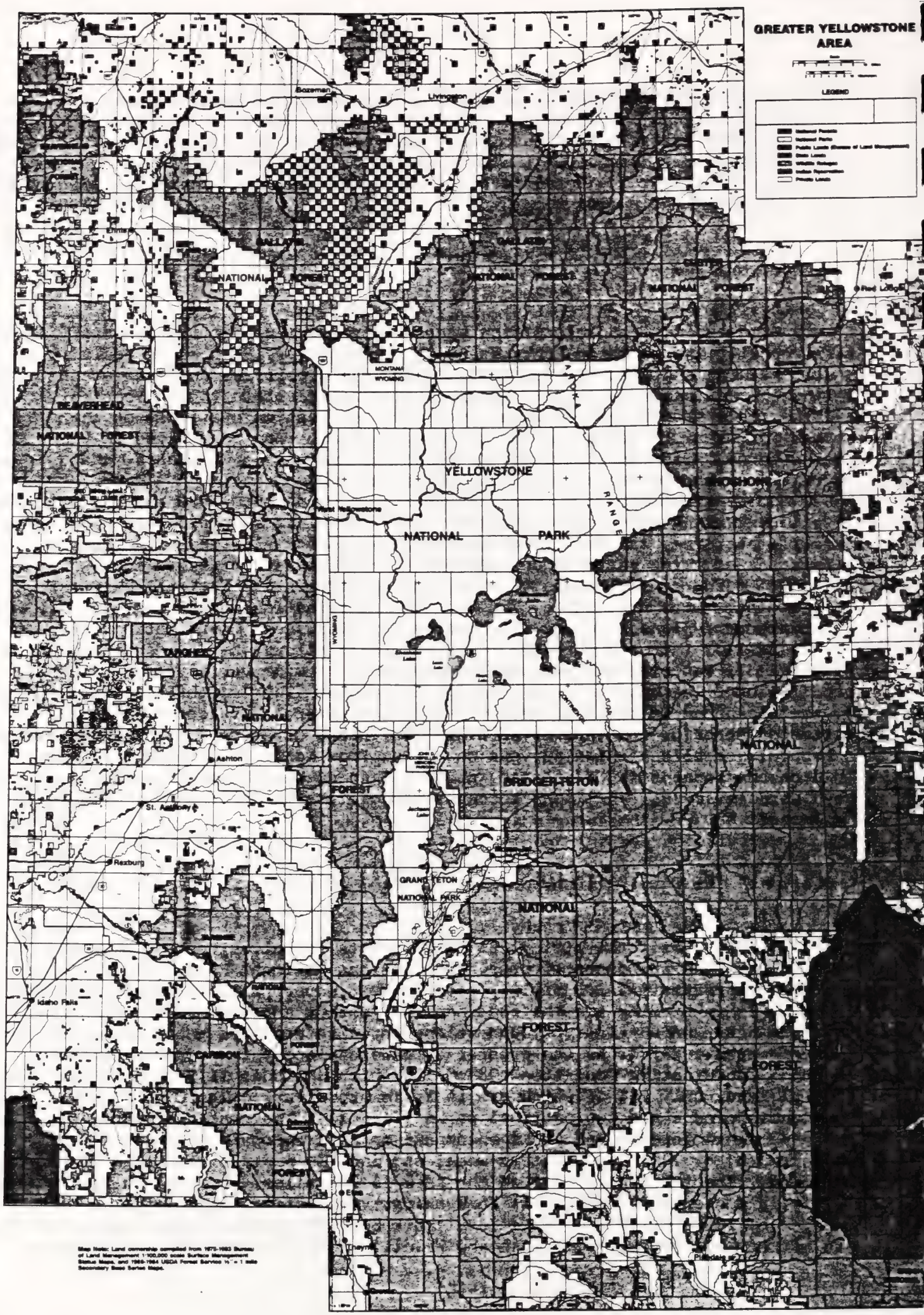
information and analysis of wolf control addresses specific questions posed by Congress. It is in no sense intended to substitute for an EIS. EIS-level analyses are more intensive and involve greater participation from the public and sister agencies. Because of the strong public interest in this issue, soliciting public input may be advisable before any final decisions are made on control and management zones.

APPROACH AND METHODS

A variety of documents and information sources were reviewed in the preparation of this report. The Northern Rocky Mountain Wolf Recovery Plan was especially helpful. Federal and state laws, regulations, agency policies and management guidelines, court cases, and solicitors' opinions that relate to wolf control within the Yellowstone area were examined. All information available on the potential for using the experimental population designation for wolves in the GYA was studied. Information on ungulate populations, hunter harvests, and state regulatory processes was provided by the wildlife agencies of Idaho, Montana, and Wyoming. The U.S. Forest Service provided up-to-date information on livestock grazing allotments. Information on ungulate seasonal ranges, hunter kill patterns, land ownership patterns, livestock allotment locations, and livestock stocking patterns on allotments was reviewed to assess the potential need for control of wolves both inside Yellowstone National Park and outside the park within the GYA. The aggregation of national park and national forest management plans produced by the Greater Yellowstone Coordinating Committee in 1987 (hereafter referenced as Greater Yellowstone Coordinating Committee 1987) was extremely valuable in providing a wide variety of information used in this report. The report entitled "The Greater Yellowstone Ecosystem" prepared in 1986 by the Congressional Research Service for the Committee on Interior and Insular Affairs, U.S. House of Representatives was also helpful. Public opinion surveys on wolves from Montana, Wyoming, Yellowstone National Park, Minnesota, and Michigan as well as national attitude surveys were reviewed. Pertinent technical literature on wolves and their prey was examined.

DESCRIPTION OF THE GREATER YELLOWSTONE AREA (GYA)

The GYA appears to meet the biological requirements of wolves because of its size, wildness, and abundance of prey. Yellowstone National Park itself consists of approximately 2.2 million acres (3,472 square miles), of which 96% is located within Wyoming and the remainder in Montana and Idaho. The park lies at the heart of a relatively undeveloped area referred to as the greater Yellowstone area (GYA) or as the greater Yellowstone ecosystem (Greater Yellowstone Coordinating Committee 1987:5-10) which includes 11.7 million acres of federal land, only 19% of which are in Yellowstone Park. The GYA includes six national forests and two national parks (Fig. 1). The contiguous portions of these national forests and parks encompass an area approximately 170 miles north to south, by 140 miles east to west, and include parts of Idaho, Montana, and Wyoming. The total perimeter of the park is 290 miles, 28 (10%) in Idaho, 114 (39%) in Montana, and 148 (51%) in Wyoming. Approximately 69% of the GYA is managed by federal agencies: National Park Service, U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, and Bureau of



Map Notes: Land ownership compiled from 1975-1983 Bureau of Land Management 1:100,000 scale Surface Management Status Maps, and 1966-1984 USDA Forest Service ½ = 1 mile Secondary Base Series Maps.

Recalamation. Some state (3%) and privately owned (24%) lands are dispersed among the federal lands, mainly along the area's perimeter, major roads, or drainage areas, and Indian reservaitons comprise 4% (Greater Yellowstone Coordinating Committee 1987). Specific government units included are portions of the Beaverhead, Custer, Gallatin, Shoshone, Bridger-Teton, and Targhee National Forests and Yellowstone and Grand Teton National Parks, including the John D. Rockefeller, Jr. Memorial Parkway. The Red Rock Lakes National Wildlife Refuge and National Elk Refuge are integral to the GYA. The Wind River Indian Reservation lies on the southeast corner of the area.

Approximately 32% of the national forest and national park lands in the GYA are designated wilderness (3,786,500 acres) with an additional 2,449,000 acres recommended to Congress for wilderness designation (Greater Yellowstone Coordinating Committee 1987:5-17, Fig. 2). Currently, almost all of the designated wilderness in the GYA is within national forests, and the majority is directly adjacent to Yellowstone National Park. Wilderness designation is made by Congress under the 1964 Wilderness Act (Public Law 88-577, 16 U.S.C. 1311 et seq.). According to the Act, wilderness is defined as undeveloped and uninhabited federal land retaining its primeval or primitive character. Once an area is designated as wilderness, it must be managed to protect its wilderness character. Activities such as road construction, timber harvest, and motorized use are generally prohibited. Activities such as camping, hiking, hunting, horseback riding, fishing, and livestock grazing are allowed in wilderness in national forests, whereas hunting and grazing are not allowed in wilderness in national parks, except in Grand Teton National Park, as provided for in the park's establishing legislation. Many wilderness areas receive heavy use; others are merely adjacent to nonwilderness lands receiving heavy use. Wildernesses (both established and proposed) are managed by either the NPS under guideline NPS-2 and Management Policies or by the U.S. Forest Service under 36 CFR, Forest Service National Policy Direction, forest plans on wilderness management, and Minimum Wilderness Management Standards.

Wildlife is abundant in the GYA, with eight ungulate species present: el: (Cervus elaphus), mule deer (Odocoileus hemionus), white-tailed deer (Odocoileus virginianus), pronghorn (Antilocapra americana), moose (Alces alces), bighorn sheep (Ovis canadensis), bison (Bison bison), and mountain goats (Oreamnos americanus) (Table 1). Population numbers fluctuate substantially primarily due to variations in winter severity (Singer and Schullery 1989). The wolf is the only original large mammal missing from the area. Ironically, through the millennia the selective pressure of predators like the wolf shaped the most impressive characteristics of these ungulates -- their keen senses, speed, size, and agility. Any of the eight ungulate species are potential prey for wolves, although elk and mule deer will probably comprise the bulk of their diet, both in terms of numbers of prey and total biomass. Although ungulates are the main prey of wolves, they also eat a variety of small mammals, birds, and other small animals (Mech 1970).

Fig. 1. The Greater Yellowstone Area showing Yellowstone National Park, Grand Teton National Park, six national forests, Bureau of Land Management (BLM) lands, state lands, wildlife refuges, Indian reservation lands, and private lands.

GREATER YELLOWSTONE AREA
LEGEND
DEERLODGE NATIONAL FOREST
BEAVERHEAD NATIONAL FOREST
GALLATIN NATIONAL FOREST
Bozeman
Livingston
Yellowstone River
Madison River
Gallatin River
Ennis
GALLATIN NATIONAL FOREST
CUSTER NATIONAL FOREST
Red Lodge
Gardiner
Cooke City
BEAVERHEAD NATIONAL FOREST
RED ROCK LAKES NATIONAL WILDLIFE REFUGE
Red Rock River
YELLOWSTONE NATIONAL PARK
SHOSHONE NATIONAL FOREST
West Yellowstone
Cody
Shoshone River
TARGHEE NATIONAL FOREST
Ashton
St. Anthony
Rexburg
BRIDGER-TETON NATIONAL FOREST
GRAND TETON NATIONAL PARK
Snake River
Idaho Falls
TARGHEE NATIONAL FOREST
CARIBOU NATIONAL FOREST
NATIONAL WILDLIFE REFUGE
Dubois
Green River
Pinedale
Thayne
Grover
CONTINENTAL DIVIDE
WIND RIVER RANGE

Hunting is not allowed in national parks, with the exception of a limited area and season in Grand Teton National Park legislated at the park's establishment to help manage the large Jackson elk herd (Smith and Robbins in prep.). Big game animals are hunted in each of the national forests, including designated wildernesses. Regulations are set by state wildlife management agencies. Elk and mule deer are the most commonly harvested species, with bighorn sheep, moose, and mountain goats being the most highly prized ungulate big game species taken (Table 2). Nearly a half million hunter-days are spent annually in pursuit of ungulate species on the federal lands of the GYA, and about 70% of that time is spent hunting elk (Table 3). The Bridger-Teton, Gallatin, Targhee, and Shoshone National Forests account for about 90% of all hunting recreation visitor days in the national forests within the GYA (Congressional Research Service 1986).

On federal lands alone, the number of elk, mule deer, white-tailed deer, mountain goats, bighorn sheep, pronghorn, moose, and bison totaled roughly 205,600 individuals in 1987 (Greater Yellowstone Coordinating Committee 1987:5-41 through 5-48, Table 1). Of all the ungulate species in the GYA, elk are the most abundant and the most significant biologically and economically (Houston 1982). Elk habitat is scattered throughout most of the GYA. On federal lands alone (including parks), there are roughly 93,000 elk. During the fall, elk migrate along traditional routes to lower elevation wintering areas. A few animals remain at higher elevations and feed on windswept areas or near thermal areas and rivers where some forage is available. Traditional calving areas are typically found along migration routes between winter and summer ranges. Mule deer are also widely distributed across the GYA, and approximately 88,000 inhabit federal lands. Bighorn sheep and moose are highly prized big game animals, and number approximately 7,700 and 6,000, respectively, on federal GYA lands. Both are more abundant outside Yellowstone National Park; about 82% of bighorns and 52% of the moose in the GYA are in the Wyoming national forests with stable or increasing populations. Some 2,200 bison live in the area, most within the park (Greater Yellowstone Coordinating Committee 1987). Condition of the range used by all ungulate species in the GYA was considered to be generally improving or stable in 1987 (Greater Yellowstone Coordinating Committee 1987). The 1988 fires are expected to produce a long-term positive effect on the range in the park, resulting in an increase in the elk herd (Singer et al. 1989); similar results may be expected in other burned over areas of the GYA.

Roughly 31,000 elk from seven to eight herds summer in Yellowstone National Park (Singer 1990, Fig. 3). In the park, elk numbers decreased by 8,000-10,000 in 1989 (Singer and Schullery 1989). Some years about 22,500 elk from four herds winter in the park, including 20,800 from the northern herd. In severe winters, nearly half of the northern herd may leave the park. Four of the park's migratory elk herds are being harvested at near maximum sustained yield: the Jackson, Sand Creek, Gallatin, and Carter Mountain herds (Singer 1990). In Wyoming, the Jackson, Targhee, and Wiggins Fork herds are increasing; the Carter Mountain and Clarks Fork herds are stable; and the North Fork Shoshone herd is decreasing (Wyoming Game and Fish Department pers. comm.).

Fig. 2. Designated wilderness and other wilderness classifications in the Greater Yellowstone Area.

Table 1. Species of ungulates present and approximate population sizes on federal lands in the greater Yellowstone area (information compiled from Greater Yellowstone Coordinating Committee 1987).

Unit	Elk	Mule Deer	White-Tailed Deer	Mtn. Goat	Bighorn Sheep	Pronghorn	Moose	Bison
Beaverhead NF	10,000	17,000	400	250	10	1,400	200	---
Bridger-Teton NF	22,500	21,400	---	---	2,435	950	2,100	---
Custer NF	800	1,600	250	400	230	15	90	---
Gallatin NF	9,800	25,000	700	650	680	70	1,200	15
Shoshone NF	16,900	12,700	286	108	3,890	1,147	782	---
Targhee NF	7,300	8,800	100	140	30	500	1,205	---
Grand Teton NP	3,000	200	---	---	90	125	225	85
Yellowstone NP	16,700	1,000	---	---	350	360	[1]	2,000
National Elk Refuge	6,400	70	---	---	---	---	30	85
Red Rock Lakes Natl. Wildlife Refuge	5	5	10	---	---	600	100	---
Totals (to nearest 1,000 or 100)	93,000	88,000	1,700	1,500	7,700	5,200	6,000[2]	2,200

[1] Information not available.

[2] Minimum figure due to lack of data from Yellowstone National Park.

Table 2. Approximate annual harvest of ungulate species on federal lands in the greater Yellowstone area (information compiled from Greater Yellowstone Coordinating Committee 1987)

Unit	Elk	Mule Deer	White-Tailed Deer	Mtn. Goat	Bighorn Sheep	Pronghorn	Moose	Bison
Beaverhead NF	700	700	10	25	1	55	15	---
Bridger-Teton NF	4,500	5,300	---	---	95	200	330	---
Custer NF	100	200	20	---	5	1	6	---
Gallatin NF	3,000	3,500	220	20	20	5	150	60[1]
Shoshone NF	3,400	1,400	36	8	100	62	57	---
Targhee NF	1,400	1,300	3	10	---	130	90	---
Grand Teton NP	600	---	---	---	---	---	---	---
Yellowstone NP	---	---	---	---	---	---	---	---
National Elk Refuge	200	---	---	---	---	---	---	---
Red Rock Lakes Natl. Wildlife Refuge	5	5	2	---	---	35	12	---
Total (to nearest 100 or 10)	14,000	12,000	290	60	220	490	660	60

[1] Nearly 600 taken 1988-1989 (569).

Table 3. Approximate annual number of days spent hunting ungulates on federal lands in the greater Yellowstone area (information compiled from Greater Yellowstone Coordinating Committee 1987)

Unit	Mule Elk	White-Tailed Deer	Deer	Mtn. Goat	Bighorn Sheep	Pronghorn	Moose	Bison	Totals
Beaverhead NF	16,500	10,000	1,000	200	500	75	75	---	28,000
Bridger-Teton NF	115,500	31,400	---	---	1,520	450	6,150	---	155,000
Custer NF	3,000	1,000	100	85	750	1	36	---	5,000
Gallatin NF	74,900	27,700	350	600	2,950	255	1,440	90	108,000
Shoshone NF	64,700	9,500	230	24	1,720	142	319	---	77,000
Targhee NF	49,400	39,800	100	40	---	810	369	---	91,000
Grand Teton NP	3,900	---	---	---	---	---	---	---	4,000
Yellowstone NP	---	---	---	---	---	---	---	---	0
National Elk Refuge	800	---	---	---	---	---	---	---	1,000
Red Rock Lakes Natl. Wildlife Refuge	30	30	10	---	---	100	60	---	200
Totals (to nearest 1000 or 100)	329,000	119,000	1,800	900	7,400	1,800	8,400	100	469,000

Other ungulate populations include 2,000-3,000 mule deer on the northern range, in and north of the park, that mostly leave the park in winter due to deep snow (Singer 1990). Mule deer use the same winter range as elk, and migration patterns are similar. Approximately 300 bighorn sheep winter on the northern elk herd winter range. Moose are found throughout the park in summer and winter, but their numbers are poorly documented, and over 2,200 bison in three herds live within the park.

The amount of prey biomass in Yellowstone National Park is enormous. However, a substantial portion of the prey in Yellowstone (especially the southerly herds) migrate out of the park to lower-elevation winter range. Some wolves may follow them and divide their time between living inside and outside the park. Wolves could either be truly migratory as in areas where they follow caribou (Rangifer caribou) migrations, or (more likely) maintain year-round territories that extend across portions of the year-round ranges of elk herds. If so, a management dilemma may exist in how to deal with those wolves. Wolves could attempt to follow members of the Jackson herd from the park to their winter range on the National Elk Refuge. They could attempt to follow the Sand Creek herd from the southwest part of the park to their wintering grounds in Idaho. Any wolves that try to follow elk to their wintering grounds outside the park could be vulnerable to killing, either legal or illegal.

Some socioeconomic impacts of wolf reintroduction are possible as the local economy of the GYA is heavily dependent on benefits and resources from federally-managed lands. The economy is dominated by tourism and other recreational land uses, including skiing, motorized vehicle use, hunting, and fishing. Commercial outfitters and guides rely on the public lands and water for a large portion of their operations. Big game hunting, with or without the assistance of outfitters, plays a substantial role in the creation of jobs in several areas, particularly in areas surrounding the Bridger-Teton National Forest and the northern part of the Shoshone National Forest. Recreation supports 14,300 jobs (80% of total) and produces $217 million in annual income. Major recreational activities include hunting, fishing, camping, picnicking, hiking, and climbing. Nine million visitor-days of recreation occur in developed sites of the GYA each year (Greater Yellowstone Coordinating Committee 1987). The presence of wolves cannot be assumed to cause negative impacts on these activities as their presence may enhance the wilderness experience and attract more use of the area. For example, Boyce (1990) noted disagreement among outfitters about the impact of wolves on that business, with some outfitters believing that wolves would enhance business.

Timber harvest for local lumber mills provides 1,900 jobs and $42 million of income (Greater Yellowstone Coordinating Committee 1987). Livestock producers in the area rely upon public lands for grazing cattle, sheep, and horses in summer to support viable year-round operations. In 1989, some 75,000 cattle, 121,000 sheep, and 1,200 horses were on grazing allotments on the six national forests in the GYA (Table 4). Grazing provides 1,300 jobs and $30 million in revenue to local economy. Mining provides less than 1,000 jobs and generates about a half million dollars of income (Greater Yellowstone Coordinating Committee 1987). (These figures are based on 1987 data, and mining probably has increased substantially since then.)

Table 4. Approximate numbers of livestock on grazing allotments on national forests in the greater Yellowstone area. Information provided by Beaverhead, Custer, Bridger-Teton, Shoshone, Gallatin, and Targhee National Forests.

National Forest	Acres in Allotments	No. Livestock/No. Permits[1] Cattle	Sheep	Horses
Beaverhead	335,352	8,825/61	5,350/4	65/17
Custer	64,000	2,030/23	0/0	0/0
Bridger-Teton	596,372	14,191/52	3,700/3	257/32
Shoshone	1,076,816	18,685/94	12,489/11	256/8
Gallatin	618,659	7,403/93	5,941/9	462/14
Targhee	1,182,130	23,734/165	93,129/89	191/33
Total	3,873,329	74,868/488	120,609/116	1,231/104

[1] Note that total number of permits, not permittees, is shown. One individual may hold more than one permit.

PUBLIC ATTITUDES AND WOLF CONTROL

National and local attitudes and expectations regarding predator control should be taken into account when considering wolf control in Yellowstone and the GYA. The level of local opposition to wolf reintroduction may generally suggest the extent of illegal killing that can be expected. Public acceptance of wolf restoration is desirable, if not necessary, especially locally. Members of the public that live, work, and engage in recreational activities in the wolf's habitat can make the difference in whether a population exists or not, at least outside of Yellowstone. Public opinion surveys in Montana and Wyoming have revealed an overall positive attitude toward wolves in both states (Bath 1987a:19; Bureau of Business and Economic Research, University of Montana 1987;Tucker and Pletscher in press). The majority of Montanans surveyed approved (52% vs. 38%) of a wolf restoration into areas of Montana, Idaho, and Yellowstone Park. However, more than half of those from rural areas did not approve (56% vs. 39%) of wolf restoration. Bath (1987a) found that most respondents from the Wyoming general public were in favor (48% vs. 34%) of wolf reintroduction, but that support diminished with increasing proximity to the park (Bath 1987b). Stock growers were adamantly opposed to wolf restoration (Bath 1987c). Bath (1987c) mentioned that several Wyoming stock growers who responded to his survey wrote supplementary comments asking where they could obtain compound 1080 (a poison) if wolves were reintroduced. Overnight visitors to Yellowstone Park supported the concept of wolf reintroduction (McNaught 1987).

Kellert (1985a, 1986) reported a strong positive perception of the wolf among all sample groups except farmers in a Minnesota survey; nonetheless, a high rate of illegal killing was occurring. About 12% of farmers and 17% of

Fig. 3. Summer and winter distribution and seasonal migration patterns of elk and mule deer in the Greater Yellowstone Area.

Map Note: The apparent differences along some unit boundaries are principally due to differences in data collection or mapping intensity by the units rather than actual differences in the resource situation.

trappers in Minnesota said they had personally killed or captured a wolf; more than 40% of farmers, hunters, trappers, and northern county residents reported knowing someone who had captured or killed a wolf. Humans are the major cause of wolf mortality in northwestern and north-central Minnesota where the human-caused annual mortality rate is reported as 0.17% and 0.29%, respectively (Fritts and Mech 1981, Fuller 1989). Wolf populations apparently can withstand a sustained harvest of up to 30% of fall populations (Keith 1983). Persecution from humans is the reason the wolf has not recovered in Michigan even though biological conditions are favorable (Hook and Robinson 1982). Poaching may be similarly high in accessible areas of the GYA, including private land. Most human-caused wolf mortalities occur in the accessible areas of Minnesota during the deer and moose hunting seasons (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Fuller 1990) simply because more people are outdoors carrying rifles. The same would likely be true in the GYA where hunter density is high except in the 2.2 million acres of Yellowstone Park and the 0.3 million acres of Grand Teton National Park where hunting is illegal (except during an annual elk reduction in the eastern portion of Grand Teton National Park) (Gingery pers. comm.). Wolves could be more vulnerable to shooting in the GYA (outside the parks) than in Minnesota and many areas of southern Canada since the mountainous or rolling terrain and sparse forest cover and understory could increase their visibility. The degree of forest cover in the six national forests surrounding Yellowstone ranges from 89% on the Targhee to 21% on the Shoshone and averages only 57% for the forests combined. The park is 80% forested. By comparison, the primary range of the wolf in Minnesota is 77% forested (Radde, Minnesota Department of Natural Resources, pers. comm.).

National surveys conducted in recent years may indicate the national public view of wolf control in the GYA. Kellert (1979, 1985b) found that attitudes of the general public on control of coyotes (Canis latrans) differed substantially from attitudes of sheep producers and cattlemen. The general public disapproved of nonspecific shooting or trapping, strongly disapproved of the use of poisons, approved of hunting only individual coyotes known (whenever possible) to have killed livestock, approved of capture and relocation of coyotes away from sheep (even though this was an expensive solution), and disapproved of paying ranchers for sheep losses out of general tax revenues (while avoiding killing of coyotes). Sheep producers and cattlemen disagreed with the general public on all of these points except on the payment issue.

Montanans surveyed did not believe that wolves would be a serious threat to big game populations; they were evenly divided on whether wolf reintroduction would cause high livestock losses (Bureau of Business and Economic Research, University of Montana 1987). Most Wyoming residents did not believe that wolves would reduce big game hunting opportunities near the park, but residents closer to the park were less decisive in that view, and Wyoming stock growers expressed the opposite opinion (Bath 1987a,b,c). A similar response pattern emerged on the question of whether wolves reintroduced into Yellowstone National Park would cause more livestock damage than they do in Minnesota. Most Wyoming residents, including residents from those counties surrounding the

park, thought wolves would not cause more damage than in Minnesota, but stock growers held the opposite view (Bath 1987a,b,c).

Approximately 58% of the Wyoming general public thought that, if a wolf killed livestock, the problem wolf should be killed, whereas about 25% disagreed (Bath 1987b:80). Most (65%) of the Wyoming Stock Growers Association agreed that reintroduced wolves should be killed if they killed livestock. By contrast, about 46% of Wyoming Wildlife Federation respondents and only about 28% of Wyoming members of Defenders of Wildlife believed that problem wolves should be killed. Over three-fourths of the Montanans polled said that ranchers should be able to shoot wolves that attack livestock on their own property, with rural Montanans favoring 84% vs. 75%) this more strongly than the general population (Bureau of Business and Economic Research, University of Montana 1987). Similar results came from the survey by Tucker and Pletscher (in press). National surveys indicated that the public favors control that is offender-specific and relatively humane (Arthur et al. 1977, Kellert 1979, Stuby et al. 1979).

Most Minnesotans surveyed supported the concept of controlling wolf depredations on livestock (Kellert 1985a). Wolves were never eliminated in Minnesota, so the public there has a long history of living with the species and is more accustomed to the reality of wolf control. The majority of Minnesotans (except farmers) strongly favored the use of humane control methods focused on individual problem animals. Most respondents disapproved of the use of poisons, elimination of wolves without proof of guilt, indiscriminate reductions in the overall populations of wolves in areas where they are abundant, or killing of pups. The most preferred wolf control procedures were eliminating individuals that had depredated livestock, capturing and relocating wolves, compensating those who had lost livestock, and training guarding dogs. Regarding the matter of controlling wolves to allow increases in deer populations, the most favored methods (except among farmers) were reductior s in the number of deer hunters or doing nothing, and the least preferred optior was reduction in the wolf population (Kellert 1985a:11).

Before leaving the subject of the public's views on wolf control, one final point deserves mention. It is conceivable that the American public is not currently prepared, and in the foreseeable future, will not be prepared for the realities of wolf control in the Yellowstone area. The comments received in response to the movement and deaths of three wolves that were relocated in a control action in northwestern Montana in September and October 1989 leads one to question whether the public is willing to acknowledge the need for control or to accept the biological realities and risks involved in wolf relocations. It appears that a major misconception exists among the public on the following difficulties and uncertainties: 1) verification of wolf depredations on livestock, 2) capture of wolves, especially specific offending wolves, and 3) survival chances for relocated wolves. Any deliberate killing of wolves or mortality of handled (i.e., relocated) wolves in the GYA may be viewed more adversely than previously envisioned. Restoration of wolves in the GYA could create still another battleground where advocates and opponents of wolf control do combat. However, in this case, the conflict would unquestionably be center

stage for the entire nation. Education on the realities of wolf control must be a part of wolf reintroduction.

THE LEGAL BASIS FOR WOLF CONTROL

Current Wolf Control Programs in the United States

The extent of wolf control possible is determined by the degree of legal protection afforded the species. The wolf is classified as an endangered species in all areas of the conterminous United States outside of Minnesota. Wolves have been protected by state law in Montana since 1975 and in Idaho since 1977. Wyoming currently lists the wolf among predatory animals, although protection afforded under the ESA supersedes less protective state law. At present, the only significant wolf control exercised within the lower 48 states is in response to depredations or to threats of depredations on domestic animals and is strongly shaped by the ESA, as amended. Extensive and controversial wolf control programs for ungulate management are being initiated in Alaska where the wolf is listed neither as endangered nor threatened.

In Minnesota, the wolf currently is classified as "threatened" (43 FR 9612, 9 Mar 1978). Litigation has played a substantial role in the history of wolf management in Minnesota (Van Ballenberghe 1974) and in the evolution of the current depredation control program there (Brzoznowski vs. Andrus 1978, Fund for Animals vs. Andrus 1978, Coggins and Russell 1982, Fritts 1982, Goldman-Carter 1983, Kellert 1985a, Sierra Club vs. Clark 1985, O'Neill 1988). Current FWS regulations applicable to Minnesota wolves allow problem wolves to be taken in Management Zones 2, 3, 4, and 5 only "in response to depredations on lawfully present domestic animals; provided that such taking must occur within one-half mile of the place where such depredation occurred and must be performed in a humane manner; and provided further, that any young of the year taken on or before August 1 of that year must be released" (50 CFR 17.40 (d)(2)). Management Zone 1 in northeastern Minnesota is a relatively undeveloped area with few livestock where no taking/control is allowed. A compensation program, funded by the state and administered by the Minnesota Department of Agriculture, has been in place since 1977 and has paid out an average of about $23,000 per year (Fritts et al. 1990, Paul pers. comm.). Until the wolf in Minnesota was downlisted from "endangered" to "threatened" in 1978, the FWS relocated problem wolves to remote areas and released them (Fritts 1982; Fritts et al. 1984, 1985). That program was not considered successful. Since 1978, the FWS has killed problem wolves (except for pre-August pups). For the period of 1975-1986, 437 wolves were captured and 262 destroyed or otherwise removed from the population; the remainder were translocated in the earlier years or released as pups (Fritts et al. 1990). The FWS conducted the program until March 1986 when control responsibility was transferred to the Animal and Plant Health Inspection Service/Animal Damage Control (APHIS/ADC). This program has generally attained the approval of both wolf conservationists/advocates and the agricultural community (O'Neill 1988). Trapping is essentially the only control method employed in Minnesota (Fritts et al. 1990).

Authorization for control of the "endangered" Northern Rocky Mountain wolf is found in Section 10 of the Endangered Species Act. The Northern Rocky Mountain Wolf Recovery Plan, signed in 1987, recommended development of a wolf control/contingency plan, in part to reduce opposition to wolf recovery in designated recovery areas (U.S. Fish and Wildlife Service 1987). The FWS has recognized that a control program must be in place in the West, and that wolf control must accompany recovery. In 1988, FWS finalized an Interim Wolf Control Plan: Northern Rocky Mountains of Montana and Wyoming (U.S. Fish and Wildlife Service 1988). An almost identical plan that would cover Idaho is also in place. These "interim" plans are intended to operate until specific management zones and objectives are established and are intended to be amended to incorporate any subsequent changes in management objectives or direction in the different zones. These control plans are based on the concept of wolf control to enhance propagation or survival of the species. Control of problem wolves is expected to reduce the hostility toward wolves that would result in illegal killing. Section 10(a) of the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 et seq.) includes a provision allowing the Secretary of Interior to permit acts otherwise prohibited by Section 9 (including the taking of endangered species) for scientific purposes or to enhance the survival of the species. Section 10 permits are required for any wolf control action, and, according to the requirements of the Act, such actions or programs must be for scientific purposes or to enhance propagation or survival of the species. Capture, relocation, or removal of wolves can be conducted by qualified federal, state, or tribal personnel under a Section 10 permit, issued by the Regional Director of the U.S. Fish and Wildlife Service. If efforts to live-capture the animals are unsuccessful and depredations continue, lethal control (shooting) may be used in accordance with control agency policy/guidelines and in consultation with the FWS (U.S. Fish and Wildlife Service 1988). The two control actions undertaken in Montana to date were a cooperative effort of the FWS and APHIS/ADC.

The Interim Wolf Control Plan (U.S. Fish and Wildlife Service 1988) includes guidelines for determining problem wolf status, conducting control actions and disposition of problem wolves. By controlling specific depredating wolves, the FWS believes that the overall survival of the species will be enhanced. Control actions will demonstrate to the public that the responsible federal agencies will act quickly to resolve depredation problems. Thus, landowner opposition to wolf recovery, which often results in indiscriminate killing, should be reduced. The conclusion of the FWS' biological opinion issued pursuant to Section 7 of the ESA on the interim plan finds that control of specific depredating wolves is not likely to jeopardize the continued existence of the wolf. To the contrary, by removing the few wolves that kill livestock and enhancing the survival chances of nonoffending wolves, the FWS believes its control program will actually contribute to the recovery of the wolf in the Northern Rocky Mountains.

If wolves were to recover naturally in the GYA or if they were reintroduced but not as an "experimental population," the FWS' Interim Wolf Control Plan (U.S. Fish and Wildlife Service 1988) would apply there. However, if an experimental population is established, a separate control plan will be required. Preparation of a special control plan would most likely be done as

part of the rulemaking process, with participation of the three states. Provisions detailing when, how, and who could conduct control actions could be written into the special rules for the experimental population. The complexion of wolf control would hinge largely on what is permissible under the experimental population designation. The potential for an experimental population designation in the GYA and the extent of control permissible under this designation are discussed below.

A variety of control methods and devices have been used on the wolf in North America. These include steel traps, pits, deadfalls, corrals, snares, set guns, hunting (various approaches), den hunting, poisoning, and airplane hunting (Young and Goldman 1944, Lopez 1978). The Canadian provinces rely largely on poisoning to protect livestock from wolves; strychnine is used in three provinces and compound 1080 in one province. Other provinces encourage hunting and trapping to protect livestock (Carbyn 1983). Some of these control methods are more specific than others. Some methods are more appropriate when conducting highly site-specific control and others more appropriate for reducing local populations, as in wolf reduction for ungulate management. Aerial hunting has been the method of choice in the large-scale wolf reduction programs in Alaska. Techniques such as poisoning and aerial hunting are highly controversial even though they may be quite effective in targeting specific problem wolves. The use of compound 1080 is now banned in the United States, and strychnine is illegal for all above-ground use. M-44's, traps which employ sodium cyanide, are commonly used in coyote control, but have not been approved by the Environmental Protection Agency for use on wolves (permission could be sought). Aerial hunting could be employed by the FWS or its subpermitees under its Section 10 permit. However, the primary methods used in the GYA are expected to be trapping (modified steel foothold traps), shooting, and live-capture via darting from aircraft in the vicinity of the depredation. Humaneness must be an important consideration in all control activities if the public is to accept wolf control in the Yellowstone area.

A major concern of grazing allotment holders and APHIS/ADC is how the presence of wolves on national forests surrounding Yellowstone would affect coyote control. Each year APHIS/ADC conducts control on certain allotments where there is a history of coyote problems. Rather than operating under permit, APHIS/ADC presents their planned work in an annual work plan. Control methods used on national forest lands are basically restricted to aerial hunting, calling and shooting, and trapping. M-44's are also among the methods used. The Northern Rocky Mountain Wolf Recovery Plan recommended APHIS/ADC activities be compatible with wolf management objectives:

> Generally in Zone I, traps for coyote control should be No. 2, (No. 3N with offset jaws in Zone II) and should be checked once every 24 hours. Aerial shooting should be limited to October through May and snares should not be used. Use of toxicants should be limited to those that avoid killing wolves either because of the selectivity of the delivery system or the toxicant. (U.S. Fish and Wildlife Service 1987:37).

Not being able to use M-44's would be a handicap to APHIS/ADC personnel. These devices are particularly useful in situations where ground conditions make trapping difficult. If APHIS/ADC was forbidden from using M-44's each time a wolf might be in the area, coyote control efficiency would be impacted (Handegard, Rightmire, Worthen pers. comm.). Thus, the presence of wolves may indeed restrict the control tools that can be used in existing control programs.

The Experimental Population Designation

The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987) recommended reintroduction of wolves to Yellowstone National Park as an "experimental population." This designation has been touted within the conservation community as providing the management flexibility needed to render reintroduction workable (Tilt et al. 1987). Considerable discussion has occurred about that possibility; however, some misunderstanding exists about what an experimental population is and how it would be regulated. The "experimental population" designation had its origin in an amendment to the Endangered Species Act in 1982. Before 1982, the FWS could reintroduce threatened and endangered species into unoccupied historical range; however, many attempts to do so were fervently resisted. The FWS lacked the ability to assure private landowners, other federal agencies, and state and local governments that transplanted populations would not disrupt their future land-management options due to the "jeopardy" prohibition of Section 7 and/or the taking prohibition of Section 9 of the ESA. Such resistance caused the FWS to abandon plans to reintroduce endangered red wolves (Canis rufus) to Kentucky and Tennessee in 1984 (Parker 1989). In an effort to encourage acceptance of reintroductions, Congress amended the ESA in 1982 to include a new Section 10(j) that allowed the Secretary of Interior the opportunity to designate reintroduced populations as "experimental." The 1982 amendment defined an experimental population as:

> Any population (including any offspring arising solely therefrom) authorized by the Secretary for release under paragraph (2), but only when, and at such times as, the population is wholly separate geographically from nonexperimental populations of the same species (Section 10(j)(1)).

A clarification further in the amendment specifies that "experimental" applies to populations derived from endangered or threatened species for which the Secretary has determined that a release will further the conservation of that species. Section 10(j)(2)(c) gives the FWS more flexibility for the management of these populations by providing that all experimental populations shall be treated as threatened species regardless of the status of the donor population. Regulations implementing Section 10(j) were published on August 27, 1984 and are codified at 50 CFR, Part 17, Subpart H. Even though 5 years have passed since publication of the final rule, there has been surprisingly little attention given the experimental population rule in papers on endangered species management (Bean 1983, 1986, 1988; Kellert 1985c; U.S. Fish and Wildlife Service 1987, 1988; Fitzgerald 1988; Greenwalt 1988).

To date, the experimental population designation has been made or proposed for nine species: red wolf , Delmarva fox squirrel (Sciurus niger cinereus), Colorado squawfish (Ptychocheilus lucius), woundfin (Plagopterus argentissimus), yellowfin madtom (Noturus flavipinnus), southern sea otter (Enhydra lutris nereis), Guam rail (Rallus owstoni), desert pupfish (Cyprinodon macularius), and Gila topminnow (Poeciliopsis occidentalis occidentalis). The sea otter reintroduction and designation was done by an Act of Congress (Public Law 99-625; Nov. 7, 1986). A bill currently in the House of Representatives (H.R. 2687) would require that an EIS be conducted to examine the feasibility of placing wolves in Yellowstone as an experimental population.

The rulemaking process for experimental populations is done in accordance with 50 CFR 17.81. Before designating a population as "experimental," the Secretary must determine through the rulemaking process that the reintroduction will further the conservation of the species, establish the geographic location of the population, and determine if such a population is essential or nonessential. Designation would include developing proposed special rules to identify the location of the experimental population, outlining procedures for its management -- possibly including special activities designed to contain the population -- and compliance with the Administrative Procedures Act which involves public review of the rulemaking and includes publishing the above in the Federal Register.

Experimental populations must be designated either "essential" or "nonessential." "Essential" refers to a reintroduced population whose loss would be likely to reduce the likelihood of the survival of the species in the wild. Essential populations receive the full protection of Section 7, meaning that federal agencies must formally consult with the FWS on actions that may affect the species (Sec. 7(a)(2)). "Nonessential" refers to an experimental population whose loss would not likely reduce the survival of the species in the wild. Except in national wildlife refuges or national parks, "nonessential" populations are treated under Section 7 as "proposed species." Thus, as provided in Section 7(a)(4), federal agencies must only consult with the FWS on activities that might jeopardize the species. A jeopardy ruling by the FWS does not prohibit the federal agency from committing resources to a proposed activity. In national parks and national wildlife refuges, they are treated as threatened species under Section 7(a)(2). Congress intended that most experimental populations be considered "nonessential" (H.R. Conf. Rept. No. 835).

As provided in Section 10(j)(2)(c) and 50 CFR 17.82, all experimental populations are treated as threatened species for which the FWS must write special rules concerning prohibited acts. Basically, the writing of special rules provides the FWS the opportunity to tailor the reintroduction of an experimental population to specific areas and specific local conditions, including specific opposition.

A summary of procedures for designating experimental populations follows (50 CFR 17.81):

1. Determine if experimental population designation is appropriate:

   A. If no local or other opposition exists, the introduction can occur without experimental population designation.

   B. If local or other opposition exists, then experimental population designation is appropriate.

2. Determine if the following criteria can be met:

   A. Suitable natural historic habitat exists within the species' probable historic range outside the species' current range.

   B. The experimental population, at least during part of the time, will be wholly separate and distinct from other nonexperimental populations.

   C. The release will further the conservation of the species.

3. Determine the essential/nonessential status of the population.

4. Develop the proposed rule to include:

   A. Background information including standard language on experimental population amendments and regulations, description of species' present status, historic distribution, reasons for decline, threats, biology, description of reintroduction area, reintroduction methods, status of parent population, and expected impact of removal of individuals from parent population.

   B. Rationale for proposing essential or nonessential status.

   C. Location of the site and factors that provide for the isolation of the population from other populations.

   D. When and how release will occur, the roles of different agencies, and how wolves will be monitored. How the species would be protected under the ESA.

   E. Special rules to allow for greater management. These can include "take" provisions and measures to keep the population from expanding beyond boundaries of the experimental population, etc.

5. Internal and public review of proposed rule, required documents, etc.

6. Prepare other required documents: Summary, Intraservice Section 7 Evaluation, Section 7 Consultation, Determination of Effect of Rules, appropriate National Environmental Policy Act documents. (Note that two FWS regions are involved in the GYA. A single set of documents should be prepared and signed by both regional directors.)

The requirements and procedures specified above would be appropriately addressed during promulgation of the proposed rulemaking and preparation of National Environmental Policy Act documents on the proposal. However, in considering the matter at this time, nothing is seen in the above requirements or procedures that would prevent reintroduction of the wolf to Yellowstone National Park or the GYA under Section 10(j) of the ESA. In fact, the experimental population designation appears to provide a nearly ideal mechanism for recovering the wolf there, assuming the states participate in management. We know from public opinion surveys, correspondence received, and statements from the public, various organizations, and the states that there is considerable opposition to reintroducing wolves in Yellowstone or the GYA. Thus, under item 1 of the summary of procedures, it is appropriate to pursue the experimental population designation. The Yellowstone area is certainly suitable natural historic habitat and is outside the species' current range. A reintroduced population there would be separate and distinct from the nearest nonintroduced population, and a release of wolves in Yellowstone would further the conservation of the species. An experimental population in Yellowstone/the GYA could receive the "nonessential" status because its loss would not appreciably reduce the likelihood of survival of the species in the wild. (Wolves are abundant in Alaska, Canada, and around 1,200 exist in Minnesota; many thousand members of the same species exist in the eastern hemisphere.) In the red wolf rulemaking, the introduced population was designated "nonessential" -- even though that species is extinct in the wild -- based upon the presence of seven captive colonies totaling 80 animals and the ease with which the species reproduces in captivity (50 CFR 17.84 (c)). With the nonessential status, federal agencies would only have to confer informally with the FWS under Section 7(a)(4) about proposed actions that would jeopardize the population. However, this would not be the case within national parks and refuges where wolves would be treated as threatened species subject to formal consultation with the FWS under Section 7(a)(2).

Development of the proposed rule would be the most critical and challenging step and would take considerable thought. A number of complex issues would have to be resolved including control measures, management zones, take provisions, and measures to keep the population within the defined area. This is where the critical question arises of how much taking is permissible under Section 10(j) and if states can join in the management of an experimental population through a plan that provides for some taking, while still meeting the definition of long-term conservation of the species. A major task would be preparation of a management plan or plans by the three states in consultation with federal agencies. Preparation of such plan(s) would likely require some change in state legislation where current state law was inconsistent with management as called for in the reintroduction plan. For example, Wyoming's listing of the wolf as a predator would have to be altered. Idaho's statutes prevent the Idaho Department of Fish and Game from being involved in wolf surveys or research and management of wolves in Idaho, including the expenditure of funds for these activities. The department is authorized to participate in wolf recovery and handle nuisance wolf problems. Montana could authorize taking, including a regulated harvest by the public without any change of statutes. All pertinent statutes and regulations of each of the three states would need to be carefully reviewed, necessary changes made, and a conservation plan would probably need to be finalized before special rules for the experimental population were published in the Federal Register. This

report attempts to lay out and discuss two issues that would be key in the special rules: control of wolves both inside and outside Yellowstone National Park and management zone options.

In considering possible reintroduction of wolves to Yellowstone National Park/the GYA, it is germane to consider the regulatory ramifications of a scenario in which wolves naturally colonize the area, i.e., without designation as an experimental population and with Sections 7 and 9 of the ESA in full effect. Wolf recovery is occurring naturally in northwestern Montana (Ream et al. 1990) which should enhance the probability of wolves reaching Yellowstone. Even now, the NPS and the FWS receive occasional reports of wolf observations from the GYA. Current sightings are thought to be primarily sightings of wild coyotes or wolves or wolf-dog hybrids that have been released or escaped from captivity (Weaver 1978:20). The possibility exists that wild wolves dispersing from Idaho or Montana could reach the area in the next few years and establish a small breeding population. Occasional reports of wolf observations are received from southern Montana, especially from along the Continental Divide west of Yellowstone (Ream and Mattson 1982). Several reports from various locations in central Idaho have led some to conclude that a small number of transient wolves exists there (Kaminski and Hansen 1984, U.S. Forest Service 1989). Travel by wolves from Idaho to Yellowstone would be perilous, but entirely possible. Wolf dispersal movements of up to 550 miles have been documented (Fritts 1983, Ream pers. comm.). The distance from Glacier National Park to Yellowstone National Park is only 300 miles, and the distance from central Idaho to Yellowstone is only 150 miles.

Assuming that wolf recovery proceeds naturally in Montana and Idaho -- as it probably will -- dispersing wolves will eventually make it to Yellowstone. The only question is <u>when</u>. Wolves that naturally colonize Yellowstone could not be designated an experimental population because the 1982 amendment refers to <u>reintroduced</u> populations. Moreover, a small population could not be augmented with reintroductions and the population be designated as experimental because the amendment stipulates that such a population (meaning animals or plants for release) must be "wholly separate geographically from nonexperimental populations of the same species" (Section 10(j)(2)). Wolves that naturally colonize Yellowstone Park/the GYA on their own would be afforded the full protective provisions of the ESA; i.e., Sections 7 and 9 would apply -- at least until they were delisted. Clearly, this scenario offers far less management flexibility than is possible through reintroduction as a nonessential experimental population. One wolf-advocate group (Earth First!) has informally stated its intent to reintroduce wolves to Yellowstone Park if government agencies do not do so. If such an illegal reintroduction were to occur, it might not be possible to determine if released animals were of captive origin, requiring they be left in the ecosystem. All concerned with wolf restoration in the Yellowstone area should be alert to this possibility. Interestingly, at least 33% of Wyoming residents surveyed believe that wolves already exist in Yellowstone National Park (Bath 1987b).

The regulation establishing an experimental population must include a description of the area where the species will be found and where it will be identified as experimental. If individuals move outside the defined area and

mingle with nonexperimental individuals of the same species, the experimental designation would not apply. Outside the boundaries of the experimental zone, wolves would be classified as endangered and be afforded the full protection of the ESA. The geographic boundary for distinguishing between experimental and nonexperimental (fully protected) populations should be made in the conservation plans and published in the Federal Register. In a zone-management system the outer perimeter of the outermost zone would define the limits of the "experimental population area." In the GYA, it may be advisable to circumscribe a very large area to allow management flexibility over all areas in which wolves might be expected to stray. In the red wolf project, it was decided that the regulations would apply over a four-county area and that animals that left the refuge would be retrieved (Parker et al. 1986). In the GYA, such wandering individuals might be managed/controlled by the states if the states were allowed to manage wolves outside the primary recovery zone(s) through a plan that provided for the long-term conservation of the species.

Taking of Experimental Populations

A key question in wolf control in the GYA is how much taking of an experimental population can be authorized. In terms of the potential for state management outside the primary recovery area, the question is crucial. The Northern Rocky Mountain Wolf Recovery Plan assumed that the experimental population designation in the GYA would give broad flexibility in controlling wolves and recommended that consideration be given to allowing livestock owners to take depredating wolves under certain conditions (e.g., verified depredations on lawfully present livestock on private property; control actions limited to within one mile of depredation site). Clarification of this issue requires examining the intent of Congress in amending the ESA with Section 10(j).

A report by the Senate Committee on Environment and Public Works concerning the 1982 amendments stated:

> The purpose of requiring the Secretary to proceed by regulation is to provide a vehicle for the development of special regulations for each experimental population that will address the particular needs of that population. The Secretary is granted broad flexibility in promulgating regulations to protect the threatened species. These regulations may even allow the taking of threatened animals.... Where appropriate, the regulations may allow for the direct taking of experimental populations. For example, regulations pertaining to the release of experimental populations of predators, such as red wolves, will probably allow for the taking of these animals if depredations occur or if the release of these populations will continue to be frustrated by public opposition. (Rept. No. 418, 97th Cong., 2d Sess. 8, 1982).

Identical language appeared in the report of the House Committee on Merchant Marine and Fisheries.

The FWS quoted the above Committee Report in its final rulemaking when addressing a question of the potential effect of a recent decision in Sierra Club vs. Clark (1984) on the less restrictive taking provisions that could apply to an experimental population under Section 10(j). In that case, the court had rejected the Secretary's assertion of authority to allow regulated taking of threatened species without showing the need to reduce population pressures on an existing ecosystem which "cannot be otherwise relieved." Widespread concern about this case had been expressed. In addressing that concern, the FWS noted in its 1984 rulemaking that congressional intent behind authorizing an experimental population release was not to relieve pressure on an existing ecosystem but to enhance the recovery potential of a listed species. The essential purpose of Section 10(j) was to provide the Secretary sufficient flexibility so that public opposition to the release of experimental populations could be avoided (49 FR 33889, August 27, 1984). Based on the legislative history, the FWS believes that the taking provisions adopted under Section 10(j) would not be restricted by the ruling in Sierra Club vs. Clark. Review of the final rulemaking certainly leaves the impression that the FWS intended broad authority for taking, if taking was necessary to win support for a reintroduction and when taking is consistent with the long-term conservation (and recovery) of the species.

In a 1987 report, the Senate Committee on Environment and Public Works reiterated its intent with regard to the flexibility for taking of experimental populations and in doing so specifically mentioned potential reintroduction of wolves to Yellowstone:

> Concerns have been raised about the potential effect of the Eighth Circuit's opinion with respect to the Fish and Wildlife Service's recovery plan for the Rocky Mountain Wolf, which proposes to introduce a population of wolves, designated as 'experimental' and treated as 'threatened' under the Act, to Yellowstone National Park. The states of Montana, Wyoming and Idaho have maintained that the court's decision regarding threatened species might jeopardize the use of public hunting or trapping to control individual wolves of the experimental population when they occur outside the Park.
>
> In 1982, Congress amended the Endangered Species Act to include a new Section 10(j) to encourage the establishment of such 'experimental populations' of endangered or threatened species. Experimental populations are populations that are purposefully introduced outside the current range of the species to further the species' conservation. Section 10(j) gives the Secretary great flexibility in designing a program for the conservation of an experimental population in order to address the particular needs of that population, including the need to avoid public opposition to the introduction of the population.
>
> Since the Eighth Circuit Court addressed the Secretary's authority to allow regulated takings of a threatened species and since Section 10(j) provides that experimental populations shall be

treated as if they were listed as threatened, some have interpreted Sierra Club vs. Clark as limiting the Secretary's flexibility in developing experimental populations regulations.

> This interpretation is wrong for several reasons. First, the court's opinion explicitly distinguished experimental populations regulations under Section 10(j) from regular threatened species regulations under Section 4(d) and, therefore, contains no ruling on the former. Second, and most important, the report by this Committee in 1982 made clear that the Secretary has sufficient flexibility to allow regulated taking of experimental populations where necessary to deal with the particular circumstances facing the population (S. Rept No. 240, 100th Cong., 1st Sess. 6, 1987).

The committee then references its 1982 report cited above and continues:

> We note with approval that, based upon identical language in the report of the House Committee on Merchant Marine and Fisheries, the Fish and Wildlife Service adopted this interpretation in promulgating regulation to implement Section 10(j) 49 Fed. Reg. 33885, 33889 (August 27, 1984). For all of these reasons, the Eighth Circuit's opinion in Sierra Club vs. Clark does not affect the flexibility granted in Section 10(j) for development of experimental population regulations (S. Rept. No. 240, 100th Cong., 1st Sess. 6, 1987).

The inescapable conclusion is that Congress' intent was to make more reintroductions possible, i.e., to make reintroduction a more viable recovery tool, with the full realization that provisions for taking may be necessary to make a reintroduction possible. No connection was intended between "regular threatened species regulations under 4(d)" and taking of experimental populations. But exactly what does this mean for wolves in the Yellowstone area?

The FWS asserts that special rules could be written and approved to allow for control of depredating wolves in the GYA. Taking would be easiest to justify if the FWS, APHIS/ADC, or states were doing the taking and if it were directed at specificly offending wolves. Taking would be harder to justify if members of the public are involved; however, there is nothing in the regulations that specifically that all taking would have to be done by government personnel (the final rulemaking for the gray wolf in Minnesota and the red wolf in North Carolina does require control be done by state or federal personnel). Allowing livestock owners to kill wolves on private property after confirmed depredations might even be possible under special rules for an experimental population if the FWS could demonstrate that taking by the public is consistent with conservation of the experimental population. This includes showing that state regulations (assuming state management) are sufficient to protect the wolf. If some control by the public in defense of property is possible, it would go far in winning support among local residents for a reintroduction. There would be many advantages to the states of Montana, Idaho, and Wyoming

being able to manage wolves under a conservation plan or plans. (Note that the term "conservation plan" would not be the same as a conservation plan used under Section 10(a)(2)(A) with respect to incidental take permits; there currently is no precedent for a conservation plan under Section 10(j)).

An environmental impact statement would seem to be appropriate to the issue of whether wolves should be restored to Yellowstone. The National Environmental Policy Act (NEPA) requires preparation of an EIS on "major Federal actions significantly affecting the quality of the human environment" (Section 102(c)). Thus, the crux of whether an EIS is warranted is found in the evaluation of the "significance" of the environmental impact. The regulations (40 CFR 1508.27) state that environmental impacts significantly affect the quality of the environment according to:

> (4) The degree to which the effects on the quality of the human environment are likely to be highly controversial.
>
> (5) The degree to which the possible effects on the human environment are highly uncertain or involve unique or unknown risks.
>
> (9) The degree to which the action may adversely affect an endangered or threatened species or its habitat that has been determined to be critical under the Endangered Species Act of 1973.

The proposed wolf reintroduction into Yellowstone National Park or the park and surrounding area appears to meet these characteristics. Therefore, an EIS seems appropriate.

The Example of the Red Wolf Reintroduction

Advantages of the Experimental Population Designation

Restoration of the red wolf to the wild was recently accomplished using Section 10(j) (Phillips and Parker 1988). That effort probably would not have been possible without the opportunity to designate the released wolves as an experimental population (Parker 1989, Parker and Phillips in prep.). In the early 1980's, the FWS attempted to reintroduce the red wolf to the Land Between the Lakes area in western Kentucky and Tennessee, a 170,000-acre recreation area administered by the Tennessee Valley Authority (TVA). A technical plan was developed for reintroduction and announced to the public in the fall of 1983. Resistance soon developed from the Farm Bureaus, various livestock associations in Tennessee and Kentucky, and owners of small livestock operations in the vicinity. The belief was widely held that the presence of a reintroduced endangered species would obstruct local projects and programs and otherwise interfere with the lives of local citizens in a significant way. This was one factor that led to abandonment of the plan to reintroduce wolves

to the Land Between the Lakes area, even though the area appeared to be biologically suitable.

In 1985 and 1986, the FWS developed a plan to reintroduce red wolves to another area, the Alligator River National Wildlife Refuge in North Carolina. By this time, regulations had been developed for designating experimental populations, and the process had already occurred with three other species. When meeting with the public to explain the plan, FWS personnel were able to stress the management flexibility afforded by the experimental population designation. The FWS was able to address many of the concerns that the public voiced -- for example, that hunting and trapping on the refuge would be prohibited due to the possibility of a wolf being inadvertently shot or trapped -- when writing special regulations for the population. The flexibility made possible by the experimental population designation was of great value in winning the support of the public and was considered by project personnel to be a major factor in accomplishing the reintroduction. No changes in state laws or regulations were necessary. The red wolf project is a model for demonstrating how the experimental population designation can be used to implement regulations that provide the wolves adequate protection, and still have minimal impact on an area and its people, thereby securing the support of the public. This was exactly what Congress intended when amending the ESA with Section 10(j).

Provisions for Control of Red Wolves

It is of interest to examine how the special rules for the red wolf dealt with taking, i.e., how the rules specified and defined prohibited acts. Red wolves were introduced as a nonessential experimental population. During the public meetings, concern about accidental taking was frequently expressed by local citizens. Hunting and trapping are common activities on the refuge where the release was to occur, and the possibility existed that a person could accidentally take a red wolf in those activities, even though they were exercising reasonable caution. The Director of the North Carolina Wildlife Resources Commission had indicated that the state would support the red wolf reintroduction so long as hunting and trapping on the refuge were not impacted. Thus, the FWS decided that when taking was unavoidable, unintentional, and did not result from negligent conduct, no prosecution would be undertaken, assuming the taking was reported immediately to the refuge manager (Parker and Phillips in prep.). Taking was allowed by federal or state officials or their designees for educational purposes; scientific purposes; enhancement of propagation or survival of the species; zoological exhibition; to aid a sick, injured, or orphaned specimen; to dispose of a dead specimen or salvage a dead specimen; or to remove an animal that represented a threat to human safety (all standard language that governs the taking of endangered wildlife), or to remove an animal that was responsible for depredations to lawfully present livestock (50 CFR 17.84 (c)). The regulation did prohibit members of the public from taking red wolves that depredate livestock or otherwise cause property damage. Individuals suffering such losses must contact the FWS or state officials who are authorized to conduct control measures. In this particular circumstance, the FWS did not consider it a burden to local livestock producers for them to report problems to officials rather than take wolves themselves. Livestock are

scarce in the area, and no losses have been reported in the first two years of the reintroduction (Parker and Phillips in prep.).

The special rules apparently have the support of the local public. Two reintroduced wolves have been legally caught in leg-hold traps set by local fur trappers. In both instances, the captures were immediately reported, and red wolf project personnel successfully released the animals. Two out of four automobile strikes were reported, and all were judged to be accidental (Phillips pers. comm.). Even though hunters have sighted the wolves on at least 20 occasions, no wolf has been purposely killed to date. Project personnel attribute this extremely significant result to the fact that traditional uses of the refuge were not curtailed because of the reintroduction program. Again, this was possible because of the Section 10(j) amendment to the ESA (Parker and Phillips in prep.).

Although there are distinct differences between red wolf management in North Carolina and gray wolf management in the GYA, the advantages of the experimental population designation in crafting a reintroduction are clear from this example.

Reintroduction by Legislative Mandate

Three years ago, a legislatively-mandated reintroduction of a threatened species occurred using the experimental population designation. Public Law 99-625, 100 Stat. 3500 (1986) dictated specifications of a plan for the relocation of southern sea otters to San Nicholas Island off the California coast. The law required that the plan be developed by regulation, in cooperation with the appropriate state agency, and that it include the specification of a relocation zone and a management (otter-free) zone and some detail of how the zones would be managed. The FWS was required to make every effort to capture any sea otter that moved outside the relocation zone and return it to the relocation zone. Any member of the experimental population while in the relocation zone would be treated as a threatened species for purposes of the Act -- except that Section 7 was to only apply to agency actions that are undertaken in the relocation zone. For purposes of Section 7 of the Act, any otter within the management zone would be treated as a member of a species that is proposed to be listed under Section 4 of the Act. Taking by the public was prohibited -- but incidental taking within the management zone was not to be treated as a violation. Basically, accomplishment of this relocation was done by legislation and regulation with the intent of insuring that certain management measures could be implemented without legal challenge. Whether the reintroduction will be successful is not yet known, the major problem being that many transplanted sea otters leave the release site (Booth 1988).

Even more recently, a bill that could require the restoration of wolves to Yellowstone National Park has been introduced in the House of Representatives (H.R. 2786) where it currently is in the markup stage. The bill, sponsored by Representative Wayne Owens (Utah) would require the Secretary, through the

National Park Service, to prepare an EIS. The EIS would address the reintroduction of gray wolves to Yellowstone National Park and adjacent public lands with completion required by December 31, 1991. The preferred alternative would be selected within 60 days of completion of the EIS, and implementation of the decision would begin within 6 months. Draft amendments that have recently been formulated would allow control of wolves by private landowners, formal public involvement in cooperation with interagency effort to delineate a Yellowstone wolf recovery area, measures and funding to isolate and contain the experimental population, and provisions for state wildlife management agencies to designate wolves outside the recovery area as big game animals and control wolves when conflicts exist with state game management goals (Kaminski pers. comm.). The impetus behind the Owens Bill is the perception that federal agencies have deliberately stalled in fulfilling their legal obligation to restore the wolf to the Yellowstone area because of local opposition. The bill attempts to:

1) move the wolf reintroduction along through the normal administrative processes

2) clarify and solidify specific matters regarding wolf management that the authors consider difficult to resolve through normal administrative processes

3) solidify points of management so they would not be challenged in court.

Examples of issues that the authors feel can best be handled with specific legislative language are involvement of state wildlife agencies in wolf management, description of zones, provisions for control, and participation of the public in control on private land.

In addition to H.R. 2786, a proposal has been circulated by Senator James McClure (Idaho) that, independent of the ESA, would mandate the placement of wolves in Yellowstone and portions of central Idaho and delist them outside those core areas (exclusive of northwest Montana) (Haywood 1989). This proposal would supersede the normal NEPA process, although public input could be obtained in another manner. This proposal differs substantially from the sea otter legislation and the Owens bill. No formal bill has been drafted at this time.

These legislative initiatives could place the NPS and the FWS in a position of implementing a GYA wolf reintroduction in the near future, with specific directives on how the task is to be accomplished and with guidelines for wolf management. An advantage of this approach is that specific provisions for management flexibility could be written in as law, thereby removing any uncertainties about management flexibility. A possible disadvantage is that the NEPA process with an EIS might be bypassed or done in retrospect as was the case in the sea otter reintroduction, and public input, important in this issue, would not necessarily be heard. Opposition may be longer-lived if the public is not able to voice its opinion on an issue that evokes such strong feelings. In addition, the public may be able to offer information and

insights that are not now apparent to the agencies and contribute significantly to the planning process. Legislation such as the sea otter legislation or the Owens bill apparently would still allow for formal public input, although stipulations may have already been made on outcomes.

CONTROL OF WOLVES INSIDE THE PARK

Background and Park Policy

Potential control of wolves within Yellowstone National Park is affected by legislation and resulting National Park Service policy. Special rules that would be written for the management of an experimental population could also regulate control activities within the park. However, the rules would likely reflect current park policy quite closely.

Yellowstone National Park was created in 1872 when Congress set aside approximately 2.2 million acres as "a public park or pleasuring ground for the benefit and enjoyment of the people." The legislation assigned the new park to the control of the Secretary of the Interior who would be responsible for issuing regulations to provide for the "preservation, from injury or spoliation, of all timber, mineral deposits, natural curiosities, or wonders within said park, and their retention in their natural condition." Other park management functions were to include the development of visitor accommodations, the construction of roads and bridle trails, the removal of trespassers from the park, and the protection "against wanton destruction of fish and game" (16 U.S.C. 21-22).

Legislation in 1894 addressed the killing of wildlife within Yellowstone National Park (16 U.S.C. 3372). Section 4 of that act stated: "all hunting, or the killing, wounding, or capturing at any time of any bird or wild animal, except dangerous animals, when it is necessary to prevent them from destroying human life or inflicting an injury, is prohibited within the limits of said park ...."

The National Park Service was created by the Organic Act in 1916 for the purpose of promoting and regulating the use of the federal areas known as national parks, monuments, and reservations, "which purpose is to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (16 U.S.C. 1).

This language lies at the heart of national park system management philosophy, and the principles in the Organic Act still guide National Park Service policy today. Section 3 of the same act allowed the Secretary of Interior to "make and publish such rules and regulations as he may deem necessary or proper for the use and management of the parks, monuments, and reservations under the jurisdiction of the National Park Service."

The same section allowed the Secretary considerable flexibility in the control of animals: "He may also provide in his discretion for the destruction of such animals and of such plant life as may be detrimental to the use of any of said parks, monuments, or reservations." (Language in the same section granted the Secretary permission to graze livestock in national parks, but Yellowstone was excluded because several members of Congress expressed concerns that commercial grazing would destroy its value as a wildlife sanctuary.)

Thus, there is an implied permission to interpret legislation in establishing policy involving control of animals. The NPS has exercised this discretion in controlling grizzly bears, black bears (Ursus americanus), elk, and bison in the park in recent times and, of course, in the elimination of the wolf from the park in earlier years. In 1915, the military administration of the park called for the removal of wolves as a means of protecting more desirable species such as elk, deer, pronghorn, and other herbivores. The practice continued when the park passed into civilian hands with the creation of the National Park Service and did not subside until 1926 (Weaver 1978, Dunlop 1983). The NPS controlled wolves in Mt. McKinley National Park (now Denali National Park), Alaska, as recently as 1943. Although difficult to understand in today's society, no contradiction with legislation was seen in the efforts to eliminate the wolf from Yellowstone. In his May 1922 monthly report, the superintendent of Yellowstone commented: "It is evident that the work of controlling these animals must be vigorously prosecuted by the most effective means available whether or not this meets with the approval of certain game conservationists" (Weaver 1978:35-36).

By 1940, Adolph Murie observed: "In line with the thought prevalent in the country today, there has evolved in the national parks the wildlife policy of basing any control of animals on thorough research" (Murie 1940:16).

Policy of the National Park Service, including biological resource management, is found in NPS Management Policies (U.S. Dept. of Interior, National Park Service, Washington, D.C. 1988). This document is revised at appropriate intervals to update and consolidate servicewide policy decisions. Pages 4.5-4.6 under "Biological Resource Management," subheading "Protection of Native Animals," describes modern NPS policy on control within national parks:

> Management emphasis will be on minimizing human impacts on natural animal population dynamics.
>
> Native animal populations will be protected against harvest, removal, destruction, harassment, or harm through human action. Individual animals within a population may be removed only when ... removal or control of animals is necessary for human safety and health or to protect property or landscaped areas ....

According to NPS Management Policies, the National Park Service relies on natural processes to control populations of native species to the greatest extent possible. However, animal populations or individuals can be controlled when they present a direct threat to visitor safety and health or to protect property. The decision to initiate a control program cannot be made arbitrarily but must be based on scientifically valid information obtained through research. Planning and implementation of control actions must comply with established planning procedures, including provisions for public review and comment. Where human/animal conflicts persist, a determination will be made of whether curtailing or modifying visitor use and other human activities might be a desirable alternative to controlling animals. The need for and results of controlling animal populations will be evaluated and documented by research studies and described in the natural resource management plan.

The document identifies other management measures that may be used as necessary including live trapping and relocation, gathering research specimens for NPS and cooperating scientists, public hunting on lands outside the park, habitat management, predator establishment, sterilization, and destruction by NPS personnel or their authorized agents. In controlling wildlife populations, highest priority is to be given to encouraging public hunting outside the parks and live trapping within parks for relocation elsewhere.

Situations That Could Warrant Limited Wolf Control in Yellowstone National Park

The only significant need for control of wolves that can be envisioned for Yellowstone National Park itself is control of occasional nuisance animals and control of depredating wolves that have entered the park. Both occasions for control are expected to be rare. Most wild wolves are extremely shy of humans. It is well documented that aggressive behavior of healthy wild wolves towards humans is extremely unusual (Munthe and Hutchinson 1978, Tompa 1983, Jenness 1985, Scott et al. 1985). Mech (in press) reviewed wolf-human interactions in North America and concluded that the few aggressive encounters that have occurred seemed to be either threats, defensive reactions, or some other kind of nonpredatory interactions; and few, if any, have resulted in serious injury. Many biologists have studied wolves at close range without being attacked (Mech 1988) and have removed pups from dens in the presence of adult wolves without incident (Murie 1944). Moreover, countless people have lived, worked, and engaged in recreational activities in wolf habitat without incident. For example, no wolf attacks have occurred during some 19,000,000 visitor-days in Minnesota's Superior National Forest (Mech in press). Thus, the prospect of wolves injuring humans in Yellowstone is extremely remote. If personal injury were to occur, it probably would be the result of a wolf losing its fear of humans. Habituation (a loss of the natural fear of humans) of some species (notably bears) within parks is a fairly common phenomenon because animals learn that humans are not a threat and cease to respond to them (Herrero 1985). Outside of parks, harassment of animals is more common. This human behavior may help reinforce animals' fear of humans or may simply act to eliminate unwary individuals.

Although wolves avoid humans with uncanny efficiency in most areas, some habituation might occur in Yellowstone over a long period. Some individual

variation exists in wolves' reluctance to approach people, objects associated with people, and domesticated animals (Woolpy and Ginsburg 1967, Fritts 1982 and personal observations, Mech 1988). Individuals that are least shy (by genetic predisposition) would ordinarily be the ones most likely to be killed and thus removed from the gene pool. The protection afforded wolves in Yellowstone and the sheer numbers of humans in the park could facilitate habituation of wolves to human presence over the long-term and precipitate situations in which wolves were perceived as a threat to human safety. (The number of park visitors from January 1-September 30, 1989, totaled 2,526,853. Vehicles entering the park totaled 853,756).

Experiences in other areas suggest that some wolves can be acclimated to approach humans after artificial feeding, as has been the case with bears, but that habituation is a slow process for most wolf populations. Some minor habituation apparently has occurred in Denali National Park, Alaska, (Mech pers. comm.) whereas little or no evidence for it has been noted on Isle Royale in the forty years wolves have been there (Peterson and Morehead 1980, Peterson pers. comm.). (Visitors are only on Isle Royale for 4 months of the year.) In a 1987 incident in Algonquin Park, Ontario, a "super-tame" wolf, after repeatedly coming near people, approached a seated 16-year-old girl in a campground. When the girl shone her flashlight in the wolf's eyes at point-blank range, the wolf bit her arm (Strickland pers. comm.). The wound was superficial, consisting of two scratches and a slight abrasion. The wolf was nonrabid. Mech (in press) stated that the behavior of this wolf suggested it had been released from captivity. Algonquin Park has recorded three "tame" wolves since its establishment in 1893. Algonquin is a 2,900-square-mile park where 60,000 people travel in the interior per year and a wolf population of 150-300 wolves exist (Strickland and Ritter 1987). Yellowstone is 1.2 times larger than Algonquin but has only 15% the number of backcountry-camper nights (32,279 vs. 211,200 in 1989). Thus, any such incidents should be even rarer in Yellowstone. The novelty of wolf human interactions can best be put into perspective by considering that in a single year (1937) 115 people were injured by bears in Yellowstone National Park (Yellowstone National Park files 1937).

Bears that pose an obvious threat to humans within Yellowstone National Park are removed. The NPS closely monitors bear activity in development areas, along roadsides, in backcountry campsites, and on trails. A permit system ensures that all overnight backcountry users receive pertinent information and that campsite assignments pass through the central office which also tracks all park bear reports. This allows effective closure of sites and backcountry areas for human safety when bears pose a threat. This system could also be adapted for wolves.

Some coyotes within Yellowstone appear to have lost their characteristic fear of humans, and the same is true for ungulates living near park facilities. Habituation of bears within the park has been a well-known problem, but this is much reduced from the past because of the strict sanitation measures now enforced. All garbage is hauled out of the park, and visitors are instructed repeatedly to store food and dispose of garbage properly. These measures should also serve to prevent situations in which wolves may become habituated after becoming dependent on garbage for food (as they are in some areas, e.g.,

parts of Italy -- Boitani 1982). Conceivably, an established population of wolves in Yellowstone would cause a reduction in the coyote population in the park, as wolves are known to kill coyotes (Carbyn 1982).

A thorough consideration of all conceivable hazards wolves may pose to park visitors must include the possibility of a diseased wolf posing a threat. Wolves are subject to many diseases and disorders, including rabies, but the incidence of rabies seems to be rare (Young and Goldman 1944, Mech 1970). Rabies in wolves has been known for several centuries, and rabid wolves will attack humans, as will any other rabid canid, including dogs. Chapman (1978) reported that rabies decimated a pack of 10 wolves in northern Alaska. An incident of a wolf attacking a man in Canada in 1942 appeared to involve rabies (Peterson 1947). In that instance, a wolf grabbed a man riding about 10 miles per hour on a railroad "speeder." After knocking the man and the vehicle from the tracks, the wolf continued its attack for about 25 minutes while the man defended himself with an ax. The animal kept attacking until three other men arrived and helped kill it. The wolf was thought to be rabid based on its lack of fear and persistence of attack. The scarcity of documented rabies cases in the writings of Canadian and American wolf biologists suggests that it is uncommon in wolves in North America. Rabies seems to be more common in wolves in the higher latitudes of this continent. Approximately 58° north latitude is the lowest latitude that rabies has been documented in North America (Mech pers. comm.), whereas Yellowstone National Park is at about 45° north latitude. Rabies has never been documented in Minnesota wolves. Nonetheless, there appears to be no reason why rabies could not occur in a Yellowstone wolf. Clearly, any rabid wolves would have to be quickly eliminated.

Wolves may also be drawn into contact with humans to attack dogs. Dogs are permitted in Yellowstone Park and in campgrounds, but they must remain on a leash; they are not allowed on trails (36 CFR 2.15 (1)). Studies in Minnesota and observations in Canada and Alaska have revealed that when wolves are intent on attacking a dog, they do not display their usual wariness of humans. To the contrary, they frequently cause alarm by their apparent boldness. Most attacks on dogs in Minnesota occurred in the dog owner's yard and occasionally in the presence of a human (Fritts and Paul 1989). When dogs are killed, they are often eaten (75% of instances in Minnesota) which amplifies the human reaction. After killing a dog, individual wolves or wolf packs may deliberately seek dogs for a few days or weeks, causing a cluster of problems. Such episodes could conceivably develop within Yellowstone National Park at lodges, campgrounds, or at residences of park employees.

The NPS would be responsible for control of nuisance wolves within Yellowstone National Park. Before wolves are reintroduced to the park, the NPS, in consultation with the FWS, could develop guidelines defining nuisance-wolf status patterned after those developed for the grizzly bear (Mealey 1986). The park could also draft procedures for determining management actions, as are now in place for the grizzly bear (Yellowstone National Park 1983). Control of nuisance wolves would include capture of the problem individual(s). A list of zoos that might accept wolves could be compiled. If the zoos could not accept wolves, the animals could be relocated to another part of the park where encounters with humans were less likely. However, relocation may have a low

probability of providing a permanent solution. Relocated wolves have demonstrated a strong tendency to return to their capture site or otherwise move long distances away from their release site (Henshaw and Stephenson 1974, Weise et al. 1975, Fritts et al. 1984). Due to the size constraints of the park, the maximum relocation distance possible is approximately 110 miles (diagonal distance), and the greatest within-park distance that a wolf could realistically be taken from its capture site is closer to 75 miles. Nuisance wolves captured within the park probably would not be released outside the park. If a wolf were to engage in nuisance behavior after being relocated once, it could be recaptured and humanely euthanized.

Potentially, a wolf may also have to be captured and/or destroyed in the event of human-caused injury. The primary example envisioned is automobile strikes. As mentioned above, 853,756 vehicles entered the park during the first nine months of 1989. The park has 370 miles of paved roads. The maximum speed limit is 45 miles per hour except for a 23-mile stretch near the northwest edge within Montana where it is 55 miles per hour. The potential will therefore exist for wolves to be struck by cars on park roads. Automobile strikes are a fairly common cause of wolf mortality in areas with paved roads; eight studies in the Great Lakes region were reviewed with the conclusion that vehicle strikes constitute an important mortality factor (Mech pers. comm.). Four of nine captive-raised red wolves that have died in the Alligator River National Wildlife Refuge in North Carolina were killed by vehicles (Phillips pers. comm.). Newly released wolves may be more susceptible to automobile strikes than those that have had more time to become familiar with the area. Wolves are occasionally injured severely but not killed outright by the impact of an automobile. If and when those instances occur within Yellowstone National Park, humane euthanization of the wolf will be appropriate (assuming complete recovery is unlikely). Euthanasia of wolves in this situation is authorized by language in the ESA and by NPS regulations and policy. Mention of these circumstances can also be covered in special rules for an experimental population as was done with the red wolf (50 CFR 17.84 (c))

Additional guidance applicable to control of wolves within the park is found in NPS-77 Draft Guidelines for Resource Management that states:

> Predators are part of the natural ecosystem. No native predator will be destroyed on account of its normal utilization of any other park animal.
>
> Control of predators that are killing livestock or game animals shall be practiced outside of the park's boundaries. Entry into the park for the purpose of controlling predators will not be permitted.
>
> The National Park Service will cooperate with the control of predators that are causing financial damage, for example, by controlling any human influenced attractant in the park which is exacerbating the problem, (for example, garbage) or by reporting a predator's departure from the park.

Using this as a guideline, it is expected that designated agents would be authorized to take wolves that were traced from a depredation site to the park. However, such an event would be extremely rare. Another possible situation in which control could occur within the park is in the unlikely event that a population of prey is about to become extinct because of wolf predation. If that situation arises, the park would want to intervene, but in such a manner as to have minimal impact on the wolves involved. Both issues could be addressed in the special rules for an experimental population.

Control of predators inside a national park was a recent major issue in Carlsbad Caverns and Guadalupe Mountains National Parks when cougars (Felis concolor) that killed livestock outside the parks would flee into the parks and avoid capture. Early in 1982, local sheep ranchers requested that New Mexico Department of Game and Fish trappers in hot pursuit of a specific problem lion be permitted to enter parklands to capture it. The Department of Interior granted permission, but before the proposal could be instituted, the NPS had to go through the standard process of developing a management plan and assessing the environmental impact of the proposal. This attracted national attention which resulted in conservation groups filing a suit seeking an injunction against the plan. In 1983, the state of New Mexico withdrew its request to enter the parklands, and the conservation groups apparently withdrew their suit. Thus, the matter was never tested in court. Although the repeat of such an episode in Yellowstone would be problematic from a legal standpoint, it is unlikely that the need to pursue a problem wolf into the park will arise since trapping near the depredation site would probably be the principal method of wolf control.

Related to the above matter of controlling specific problem wolves that move into the park, the following problem could arise. At least early in a wolf restoration effort, all or most wolves in the GYA would be radiocollared, possibly with capture collars (radio-dart collars) (Mech et al. 1984, Mech et al. in press). If a radiocollared wolf was known to commit depredations, the collar could be useful in the pursuit and capture of the individual and conceivably could allow a wolf to be followed into the park. Based on control efforts involving collared wolves in Alaska and use of radiocollars in killing two Carlsbad mountain lions after they had left the park, a segment of the public might view use of the collars as providing an unfair advantage to the control agents.

Summary

Restoration of the wolf to Yellowstone National Park is in keeping with the original intent of Congress in establishing the park, basic to the purpose of national parks, and consistent with the current objectives of the NPS. No control of wolves would occur inside the park except as necessary to deal with nuisance animals and to take specific individuals that had depredated outside the park and subsequently moved within or to aid injured or sick individuals. Nuisance status would have to be specifically defined and a protocol established for controlling nuisance wolves, much like that currently in place for grizzly bears. Few wolves would engage in activities that would require

their control. NPS personnel would conduct the required control activities. The type and extent of control that will be needed is permissible within the present statutes, regulations, and policies of the NPS and could be included in the special rules that would be written for an experimental population.

CONTROL OF WOLVES OUTSIDE THE PARK

Situations That Could Warrant Wolf Control

A major question concerning recovery of wolves in the GYA is whether the primary recovery area (or experimental population area) would be limited to Yellowstone National Park or would include all or portions of surrounding public lands. Whatever the answer, there is agreement that all wolves or their offspring placed in the park will not remain within park boundaries indefinitely. Wolf packs, or more likely nonterritorial/loner wolves, may follow their prey to their winter range outside the park. Differences of opinion exist among biologists on whether Yellowstone's wolf packs would be migratory (Koth et al. 1990). No analogous ecosystems exist for comparison. In the most similar wolf-prey systems in Canada, some seasonal altitudinal movement of wolves does occur (Cowan 1947). Unfortunately, little information was obtained on this subject when wolves occupied the GYA, although some wolves definitely denned within the park. Weaver (1978) cited some evidence that wolves did follow their prey:

> Some wolves in Yellowstone apparently followed the ungulates in their altitudinal migrations to and from summer and winter ranges. Bailey (1930) reported that 'during the summers of 1914 and 1915 they [wolves] ... were following the elk herds to the high pastures of Mirror Plateau, returning with them in winter to the valleys along the Lamar and Yellowstone Rivers.'
>
> The Superintendent's Monthly Reports during 1918 state: "Towards the end of the month [May] the wolves seemed to leave the Specimen Ridge district and have not been much in evidence since. They were considerably in evidence in Slough and Hellroaring Creeks [November]."
>
> Although some wolves wintering in the Lamar and Yellowstone valleys moved toward Mirror Plateau and Pelican Valley during summer, others may have headed north out of the park. (Weaver 1978:18-19)

Whether wolf packs will move extensively with their prey on a seasonal basis, dispersing individuals will certainly travel outside the park. The individuals that are released in Yellowstone might travel long distances outside the park in an effort to return home (Henshaw and Stephenson 1974, Weise et al. 1975, Fritts et al. 1984, Fritts and Bangs personal observations in Montana). The likelihood of such movement probably can be reduced with proper release

techniques. Nonetheless, fitting all released wolves with radio-dart collars should be considered to facilitate recapture and return to the park if necessary (Mech et al. 1984, Mech et al. in press).

With the exception of Grand Teton National Park and lands administered by the FWS, GYA lands outside Yellowstone National Park are managed for multiple use, and it is here that conflicts may arise between livestock producers, wildlife managers, and hunters. Whereas national parks were founded on principles of preservation, Congress has mandated that national forests be managed for multiple use such as recreation, wildlife, grazing, mining, oil and gas, watershed, timber, and wilderness. The Endangered Species Act of 1973, as amended, nonetheless requires all federal agencies to carry out conservation (recovery) programs for endangered and threatened species (Section 7(a)(1)) and to insure that agency actions are not likely to jeopardize the continued existence of listed species or adversely modify or destroy their critical habitat (Section 7(a)(2)). Differing management objectives inside and outside of Yellowstone National Park, the potential for conflict, and the involvement of several federal and state regulatory agencies add to the complexity of reaching a satisfactory compromise on the issue of wolf control on nonpark lands. On the more positive side, wolf management should not lead to land-use restrictions such as those required for grizzly bear management due to the biological and behavioral differences between the two species. Section 7 consultation will not be an issue outside the park because of the nonessential experimental designation of the wolf population. (Within the park, formal Section 7(a)(2) consultation will be necessary.) Biologically, wolf recovery should be easier to accomplish because the reproductive rate of wolves is such that the loss of an individual (or even a pack) will be of minor significance compared to the loss of a single reproducing female grizzly bear. Therefore, removal of wolves from the population for control purposes is not analogous to removal of bears. Moreover, the reproductive potential of wolves is such that recovery levels potentially could be reached faster. There are two primary circumstances that may require some form of wolf control outside the park: 1) depredation on livestock and 2) predation on game animals.

Depredations on Livestock

The problem of wolves killing livestock is as old as animal domestication itself. Selective breeding of domestic ungulates has emphasized meat production or other characteristics useful to man at the expense of predator avoidance abilities. Wherever wolves and domestic animals have coexisted in North America, some degree of depredation has occurred. Historically, the severity of this problem in the West has been grossly overstated (Lopez 1978:182). Nonetheless, livestock depredation was one primary reason that wolves were eliminated from the West less than a century ago (Young and Goldman 1944, Lopez 1978).

Any sort of objective inquiry into the nature and extent of wolf depredations on livestock is a recent phenomenon. The level of depredation has been remarkably low in Minnesota, Alberta, and British Columbia where this problem has been studied in detail (Fritts and Mech 1981, Fritts 1982, Bjorge and

Gunson 1983, Tompa 1983, Fritts et al. in press). During the 1975-1986 period, verified complaints of depredations in Minnesota averaged 30 per year, and an average of 21 farms were affected annually (about one out of every 340 farms in wolf range). During winter, cattle and sheep are confined or their movements are restricted to areas near farm buildings, but in late April or May they are released to graze in open and wooded pastures until about October. Cattle (mostly calves), sheep, and domestic turkeys are the most common domestic prey in Minnesota. Annual verified losses of cattle averaged 4 cows, 19 calves, and 49 sheep from 1979 to 1986 (Fritts et al. in press). Wolf depredations on livestock were highly seasonal; cattle losses peaked in May and sheep losses in July-September. The number of losses was related to animal husbandry practices and to the severity of the winter prior to the depredation season (Fritts 1982, Mech et al. 1988, Fritts et al. in press). Most wolves clearly utilized wild prey even when the wolves lived near livestock. Although the effect on livestock production in Minnesota as a whole was negligible, each year a few individual producers were seriously affected. During 1975-1986, an average of 34 wolves per year were captured, and 27 per year (2% of winter-level population) were destroyed in control activities in Minnesota out of a population of about 1,200 wolves.

In Canada, most depredations on domestic animals occur in Alberta and British Columbia because of the proximity of wolves and livestock operations in those two provinces (Carbyn 1983). In Alberta during 1972-1981, there were an average of 140 wolf depredation complaints per year. Approximately 44% (61) of these complaints were approved for compensation. During 1974-1980, 365 claims were approved for indemnity payments: 67% confirmed, 18% probable, and 15% missing (Gunson 1983). Bjorge and Gunson (1983) studied wolf-cattle relationships on remote grazing leases in the Simonette River area of northwestern Alberta. Wild ungulates formed the bulk of the diet there even though wolves had free access to cattle. Of 9,425 cattle grazed during 1976-1980, a total of 299 (3.17%) were lost. Known wolf kills and maulings totaled 16 (0.17%) and 51 (0.54%), respectively. Annual wolf depredations averaged 13 cattle, but it is unlikely that all kills were detected. The primary control method was poisoning with strychnine. An average of 88 wolves per year were removed for depredation control out of a population of perhaps 5,000 from 1972-1980 (Gunson 1983).

In British Columbia during 1978-1980, an average of 144 wolf depredation complaints were confirmed each year (Tompa 1983). In addition to kills, some of the complaints involved harassment, missing animals, and maulings. Verified wolf-related losses in all stock classes were consistently less than 0.1% of stock populations in the province. A total of 455 wolves were taken in control actions during 1978, 1979, and 1980 out of a provincial population estimated at 6,300. Poisoning, shooting, and trapping were the main control methods used (Tompa 1983).

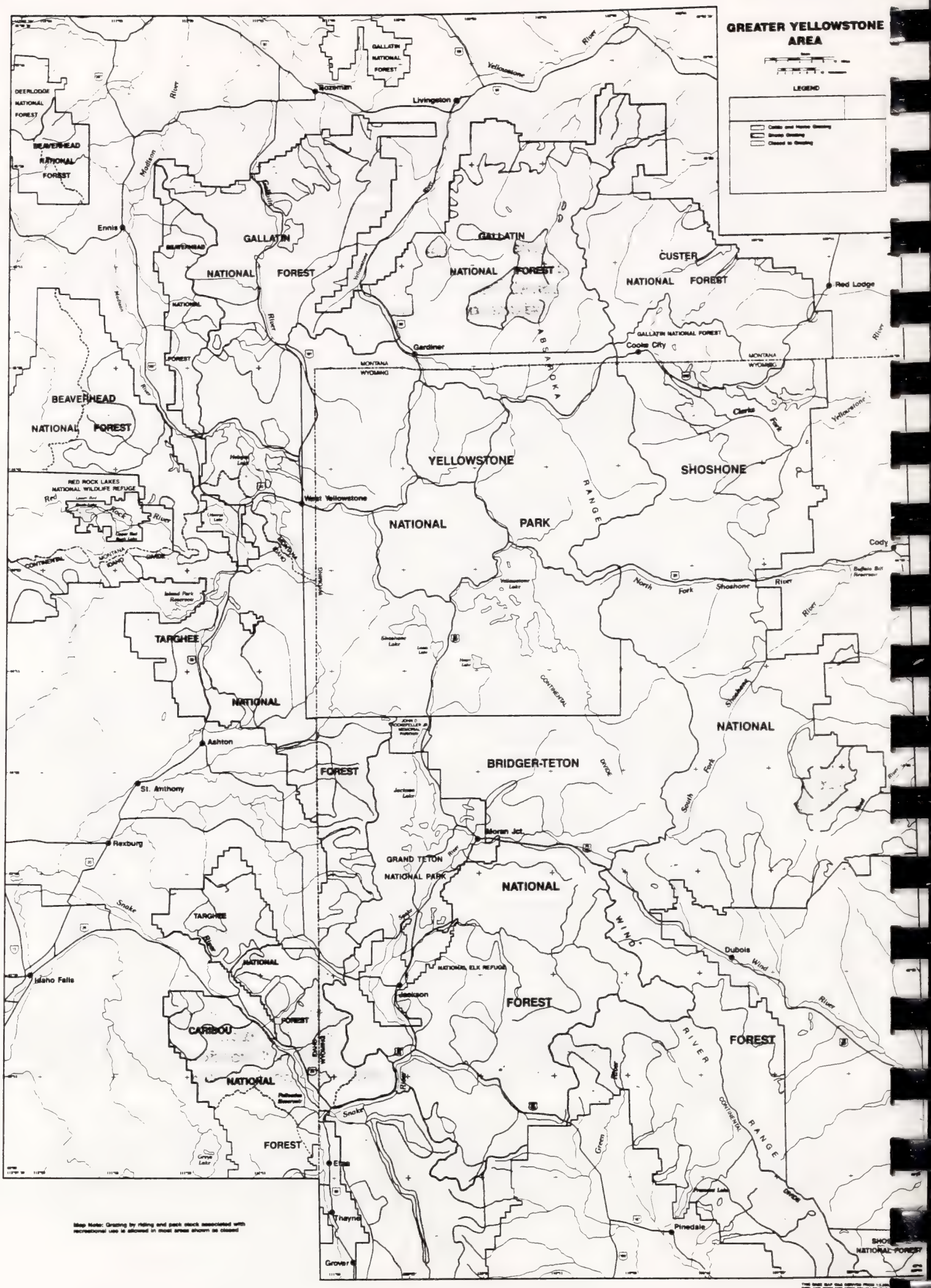
In the GYA, the greatest potential for depredation on livestock will be on the grazing allotments of the six national forests that surround Yellowstone National Park. Slightly more than one half of the national forest land is open to cattle and sheep grazing. Considering the GYA as a whole (including the park), about 44% is open to grazing, with grazing occurring primarily in

portions of those forests most distant from Yellowstone National Park (Fig. 4). The number of livestock on allotments in 1989 was 74,868 cattle, 120,609 sheep, and 1,231 horses (Table 4). There are more sheep on allotments in the GYA than on Minnesota farms, but there are fewer cattle than in Minnesota. Based on the Minnesota studies, sheep are more likely to be preyed upon by wolves than cattle and horses. Therefore, the greatest potential for depredation may be on the Targhee National Forest which had 93,129 sheep (89 permits) on allotments in 1989, followed by the Shoshone where there were 12,589 sheep (11 permits). The density of livestock, particularly sheep on public and private land southwest of Yellowstone National Park, causes the potential for conflicts to be higher there than on other sides of the park.

Most livestock in the GYA are not placed on grazing allotments until at least mid-June. The average date cattle are placed on allotments varies from June 13 on the Bridger-Teton Forest to July 3 on the Gallatin, and averages June 26 for the six national forests. The average time on allotments is 101 days (Table 5). Calving occurs prior to movement onto allotments. In Minnesota, depredation on cattle (80% of cattle losses are calves) peaks in May when most calves are still very small (Fritts et al. in press). Forty-three percent of the complaints involving verified depredations on cattle in Minnesota occur prior to June 26. Larger calves and adult cattle are more capable of eluding wolves. Therefore, the possibility exists that depredations on cattle in the GYA would be minor because most calves are already past the size of greatest vulnerability when they are placed on allotments. On the other hand, cattle losses peak in mid to late summer in Alberta and British Columbia (Gunson 1983).

Sheep are placed on grazing allotments later than cattle, with national forest averages ranging from July 3 on the Gallatin to July 17 on the Beaverhead and averaging July 10 for the six national forests combined. Sheep are present on allotments for a briefer period than cattle (x = 67 days vs. 101 days). Unlike cattle, which are unaccompanied on allotments, sheep are accompanied by herders who keep them moving to prevent overgrazing. The presence of herders may deter depredations by wolves (Curnow 1969:36). Wolf depredation on domestic sheep is greatest in July, August, and September in Minnesota, corresponding to the period of availability on the national forests in the GYA. Because depredation on sheep usually involves more individuals killed over a shorter period than cattle (Fritts et al. in press), it would be especially important to respond quickly and implement control measures promptly when sheep are being preyed upon.

Predator losses on GYA grazing allotments run less than 1% for cattle and about 5% for sheep. About half of all livestock losses are attributed to predators, and coyotes are probably the primary predator. Bears and golden eagles (Aquila chrysaetos) also kill some domestic animals (Congressional Research Service 1986:90).


GREATER YELLOWSTONE AREA
LEGEND
Cattle and Horse Grazing
Sheep Grazing
Closed to Grazing
Map Note: Grazing by riding and pack stock associated with recreational use is allowed in most areas shown as closed.
GALLATIN NATIONAL FOREST
BEAVERHEAD NATIONAL FOREST
CUSTER NATIONAL FOREST
YELLOWSTONE NATIONAL PARK
SHOSHONE NATIONAL FOREST
BRIDGER-TETON NATIONAL FOREST
TARGHEE NATIONAL FOREST
CARIBOU NATIONAL FOREST
GRAND TETON NATIONAL PARK
RED ROCK LAKES NATIONAL WILDLIFE REFUGE
NATIONAL ELK REFUGE
Bozeman
Livingston
Ennis
Red Lodge
Cooke City
Gardiner
West Yellowstone
Cody
Ashton
St. Anthony
Rexburg
Idaho Falls
Moran Jct.
Jackson
Dubois
Pinedale
Ellis
Thayne
Grover
MONTANA
WYOMING
IDAHO
Madison River
Gallatin River
Yellowstone River
Clarks Fork
North Fork Shoshone River
South Fork Shoshone River
Snake River
Green River
Wind River
Continental Divide
Absaroka Range

Indemnity programs exist for livestock lost to wolves in Minnesota (Fritts 1982, Fritts et al. in press), Alberta (Gunson 1983), Ontario (Kolenosky 1983), and in Italy (Boitani 1982). Although dealing with instances of "missing" livestock is a common difficulty, compensation programs are generally deemed successful and well worth the cost. Relations with the agricultural community are unquestionably strengthened by these programs. Defenders of Wildlife is currently raising funds for a program of compensation for wolf depredations in the Yellowstone area and elsewhere in the Northern Rockies (Fischer 1989, Task 376 of the Northern Rocky Mountain Wolf Recovery Plan - U.S. Fish and Wildlife Service 1987:36). In Montana, ranchers have already been paid a total of $4,900 for losses to wolves in depredation events in 1987 and 1989 (Fischer pers. comm.). Nonlethal methods of reducing losses of livestock to wolves might play some role in the GYA. For example, the modification of livestock husbandry practices and the use of guard dogs might help to minimize losses in some situations (Fritts 1982), although implementation of such measures may be difficult on remote grazing leases.

The seasonal migration of prey and the possibility of wolves following prey between winter and summer range presents a hypothetical depredation scenario that does not exist in most other areas of North America. If wolves follow elk outside the park to wintering areas in lower elevations, the wolves could find themselves bound to such areas past the time when elk return to summer range. Wolves breed in late February and pups are born in late April. Pups are not mobile enough to travel far until midsummer. Wolves, therefore, might not be able to move to ungulate summer range until midsummer and could be forced to prey on local livestock if natural prey are scarce (Curnow 1969:33, Edgar and Turnell 1978:76). This is what may have occurred in a depredation incident east of Glacier National Park in 1987 if the wolves involved were from the park (their origin is unknown).

When depredations on livestock occur, control actions are imperative. Provisions must be in place to deal quickly and effectively with offending wolves, both to solve the local problem and to avoid public perception of government inaction. Leaving problem wolves in the population may exacerbate the level of wolf-livestock conflicts in the long run. Livestock-killing wolves should not be the building blocks of a GYA wolf population. Wolf-human conflicts will precipitate illegal killing of wolves by the public, regardless of the penalty.

If wolves become established in the GYA, some individuals will eventually prey on livestock and others will appear to threaten the welfare of livestock and pets. The exact level of depredation cannot be predicted but probably would be small if findings in Minnesota and Canada can be extrapolated to the GYA. Losses very likely will be low, at least during the early years of recovery, because of the small numbers of wolves present and the availability of an abundant natural prey base.

Fig. 4. Areas grazed and areas closed to livestock grazing in the GYA.

Table 5. Dates cattle and sheep go onto and off of grazing allotments and duration of grazing period on National Forests in the greater Yellowstone area. Calendar and Julian dates used.

National Forest	Cattle	
	Date On	Date Off
Beaverhead	6/27 - 178	9/30 - 273
Gallatin	7/3 - 184	10/6 - 279
Custer	7/1 - 182	10/3 - 276
Bridger-Teton	6/13 - 164	10/15 - 288
Targhee	6/25 - 176	9/30 - 276
Shoshone	6/26 - 177	10/8 - 281
Averages	6/26 - 177	10/5 - 278
	Average time on allotments = 101 days	

National Forest	Sheep	
	Date On	Date Off
Beaverhead	7/17 - 198	9/15 - 258
Gallatin	7/3 - 184	9/11 - 254
Custer	no sheep	no sheep
Bridger-Teton	7/6 - 187	9/30 - 273 (2 permittees)
Targhee	7/10 - 191	9/15 - 258
Shoshone	7/16 - 197	9/4 - 247
Averages	7/10 - 191	9/15 - 258
	Average time on allotments = 67 days	

Predation on Ungulates

Predation on wild animals that man desires for meat and/or sport is another major factor leading to intolerance of the wolf (Mech 1970). Wolves coevolved with their prey species, resulting in capture abilities of predator and escape strategies of prey being well matched. While wolves are very adept predators, their prey are, on average, comparably adept at detecting them and eluding capture. This "balance" in capabilities has allowed ungulate species to persist over the millennia despite constant predation pressure from wolves and other predators. Predators such as the wolf played a major role in the development and maintenance of the anatomical, physiological, and behavioral adaptations of ungulates that make hunting them a "sport."

Reducing the number of wolves to increase hunter opportunity is more controversial than control to protect domestic animals. Alaska and the western Canadian provinces have been sites of debate and litigation on this issue over the past several years (Harbo and Dean 1983, Haber 1988, Williams 1988, Kerasote 1989). State and provincial wildlife agencies have been taken to task on wolf control programs, and data used to support control has been heavily scrutinized by other wildlife professionals and conservation groups. For example, representatives of both the Wildlife Society and the Canadian Society of Zoologists contested the validity of data used to justify wolf control in the Yukon and British Columbia (newsletter of the Canadian Society of Environmental Management 1984).

Even among wolf biologists, there is considerable discussion about the exact impact that wolves have on populations of their ungulate prey. The impact of wolves is difficult to measure and difficult to distinguish from other factors influencing prey population dynamics. Many years of study may be necessary to assess the effect of wolf predation. Apparently, wolves have different effects in different circumstances (Mech 1970, Mech and Karns 1977, Fritts and Mech 1981, Gasaway et al. 1983, Keith 1983, Taylor 1984, Messier and Crete 1985, Theberge and Gauthier 1985, Van Ballenberghe 1985, Gauthier and Theberge 1987, Bergerud and Ballard 1988, Peterson and Page 1988). Other sections of this report address that question as it pertains to Yellowstone, but the answer cannot be known until the wolf is present and then only after many years of study. Any effect would not be perceivable for some time. The return of wolves to Yellowstone would provide a rare opportunity to add greatly to the understanding of how wolves influence an ecosystem, and that opportunity should not be wasted (Taylor and Walters 1989).

Research into wolf ecology in some areas of North America has suggested that, at least in certain circumstances, wolves can play a role in depressing ungulate populations (Gauthier and Theberge 1987) and affecting hunter opportunity. This can happen, for example, after some other environmental factor such as weather, habitat deterioration, or overhunting has already depressed ungulate levels. In these circumstances, wolves can accelerate the rate of decline of a prey population and suppress it longer and at a lower level than would be the case in the absence of wolves. Such conditions are not the norm in North America. Many wolf-bear-prey systems are exploited by

hunters without driving the ungulate population to low levels. For example, the wolf has returned to the Kenai Peninsula in recent times with no perceptible effect on ungulate levels or hunting regulations. In fact, a successful caribou reintroduction has been conducted subsequent to wolf recovery (Kenai National Wildlife Refuge unpubl. data).

There are situations where wildlife management agencies may legitimately try to restore suppressed ungulate populations to a former higher level and/or raise harvest levels. This is not normally a concern inside Yellowstone National Park because of NPS management objectives. It is a concern outside the park because hunting of big game is prevalent in the national forests, wildlife refuges, and private lands in the GYA. Hunter-days in the GYA (federal lands only) total almost a half million annually, with eight big game species harvested (Table 4). The livelihood of some local people is tied to hunting, and any level of wolf predation on big game may be construed as a threat to their economic well being.

In addressing wolf predation on a herd that is declining, state wildlife agencies will have four options available: 1) reduce the hunting kill, 2) reduce wolves, 3) at best, do both 1 and 2, and 4) do nothing. The public response to option 2 is predictable. Given the case history in Alaska and elsewhere, some hunters will demand wolf reductions. A large segment of the public will oppose reduction of wolves at nearly every level, but especially if it is justified on the basis of providing more ungulates for the hunter (Van Ballenberghe 1989). Biologically, there is no reason wolf reduction should not occur if it is done in such a way that the survival and viability of the overall wolf population in the area is not jeopardized.

Because some populations of prey that may be used by wolves are already harvested at nearly maximum sustained yield (Singer 1990), it may indeed become biologically prudent to reduce wolf populations in some areas of the GYA. To introduce the wolf is to interject a new variable into the already complex task of managing populations of ungulates outside the park. Wolves should be managed in ways compatible with state objectives for ungulate management, consistent with the long-term conservation of the wolf. Wolf and ungulate management cannot be treated as separate issues but must be effectively integrated, as recognized by task 382-1 of the Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987:36).

The foremost problem in administering wolf control for ungulate production will be determining or defining the exact circumstances in which wolf reduction should be practiced (Task 37 of the Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987:33)). Criteria must be established in advance for determining when control should occur in order to remove as much subjectivity as possible from decision making. The location of the control actions and numbers to be taken would need to be clearly identified and enforced in order for the desired results to be achieved. Criticism and litigation for killing wolves can be expected in the absence of data that show the action is warranted, i.e., that it would have the desired effect on the ungulate population. Thus, fairly in-depth understanding of the

wolf-prey-hunting relationship in the GYA would be highly desirable. On the other hand, there have been enough studies of wolf control in Alaska and Canada to allow some generalizations and guidelines without definitive data each time control is to be exercised. In a statement of the IUCN Wolf Specialist Group on wolf control, the group stated:

> The control should be carried out after sufficiently scientifically collected data are gathered indicating the need. The Group also recognizes that it is not always possible, feasible, necessary, or desirable to wait until a completely definitive study is conducted in each instance before control is instituted. As increasing amounts of data are collected from various regions, it is scientifically valid to generalize and draw inferences from previous studies and apply them to current situations so long as the limitations of such an approach are recognized (Wolf Specialist Group, IUCN/SSC 1984).

Consistent with this statement, a wolf-prey study prior to each control effort for ungulate management in the GYA should not be necessary or reasonable.

OPTIONS FOR MANAGEMENT OF WOLVES IN THE GREATER YELLOWSTONE AREA

Control Options and Management Zones in Concept

As stated earlier, wolf control and wolf management zones are inseparable topics; therefore, the two are discussed together. Again, the objective is not to make specific recommendations about how control programs should be structured or about specific management zones. Instead, the intent is to identify some of the many options available and list some of the major advantages and disadvantages of each.

The possibilities for control of wolves in the GYA could be portrayed as points along a continuum (Fig. 5). The continuum could stretch from very intensive control, including the taking of wolves by the public immediately outside the Yellowstone National Park boundary, to essentially no control anywhere within the GYA. Historically, the level of wolf control practiced in the GYA was off the right end of the scale (Young and Goldman 1944, Lopez 1978, Weaver 1978). Control programs of past eras in the West had the objective of eliminating the wolf, and control methods were used in the area (now the GYA) that will not be seen again (aside from the fact that we are now dealing with a national park). The control possibilities of the late twentieth century are of a different magnitude with different objectives and should not be confused with the wolf control of earlier times.

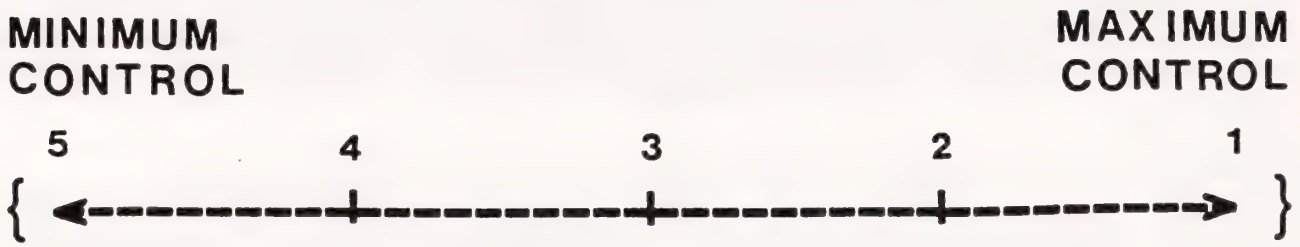


Fig. 5. Management/zone possibilities in the GYA as a continuum representing 5 specific management/zone scenarios described.

As we move right along the line toward more control, the potential for conflicts with big game management and livestock production decreases. A management scheme toward the left end of the scale should mean fewer conflicts but may also mean longer time for population recovery, lower overall population size, and greater risk to the population. Clearly, the possibilities for levels of control are numerous. The degree of control that is optimal for balancing opposing objectives and interests in the GYA probably lies somewhere between these extremes.

The objectives behind management zones are to provide for different management in different areas and/or in different circumstances to meet specific goals and objectives (Fig. 6). Zone management of wolves may or may not be preferable in the GYA. A number of assumptions are inherent in the concept of zone management for wolves: 1) there are places that wolves belong and places they do not belong because of potential conflicts with man, 2) adequate habitat to support a viable population should exist in the zone or zones where the spec es is afforded the most protection, and 3) the species should receive high priority in the central zone (i.e., zone with most protection, but other activities are of higher priority in the outer zone(s)). The Northern Rocky Mountain Wolf Recovery Plan recommended management by zones but assumed zones would be developed during a NEPA-type process. Three zones were recommended in the Recovery Plan for each of the three Northern Rocky Mountain wolf recovery areas; the extent of control was expected to be greater in the higher numbered zones:

> Management Zone 1: This zone should contain key habitat components in sufficient abundance and distribution on an annual basis to sustain 10 breeding pairs of wolves. It should generally be an area greater than 3,000 contiguous square miles with less than 10% private land (excepting railroad grant lands) and less than 20% subject to livestock grazing.
>
> Management Zone 2: This zone should be established as a buffer zone between Zone 1 and Zone 3. It should contain some key habitat components but probably not in sufficient abundance and distribution on an annual basis to sustain a viable wolf population. Zone 2 boundaries may be changed according to demonstrated wolf population and habitat needs, provided the change does not bring wolves into conflict with existing livestock areas/allotments.

Management Zone 3: This zone contains established human activities such as domestic livestock use or other human activities or developments in sufficient degree to render wolf presence undesirable. (U.S. Fish and Wildlife Service 1987:31)

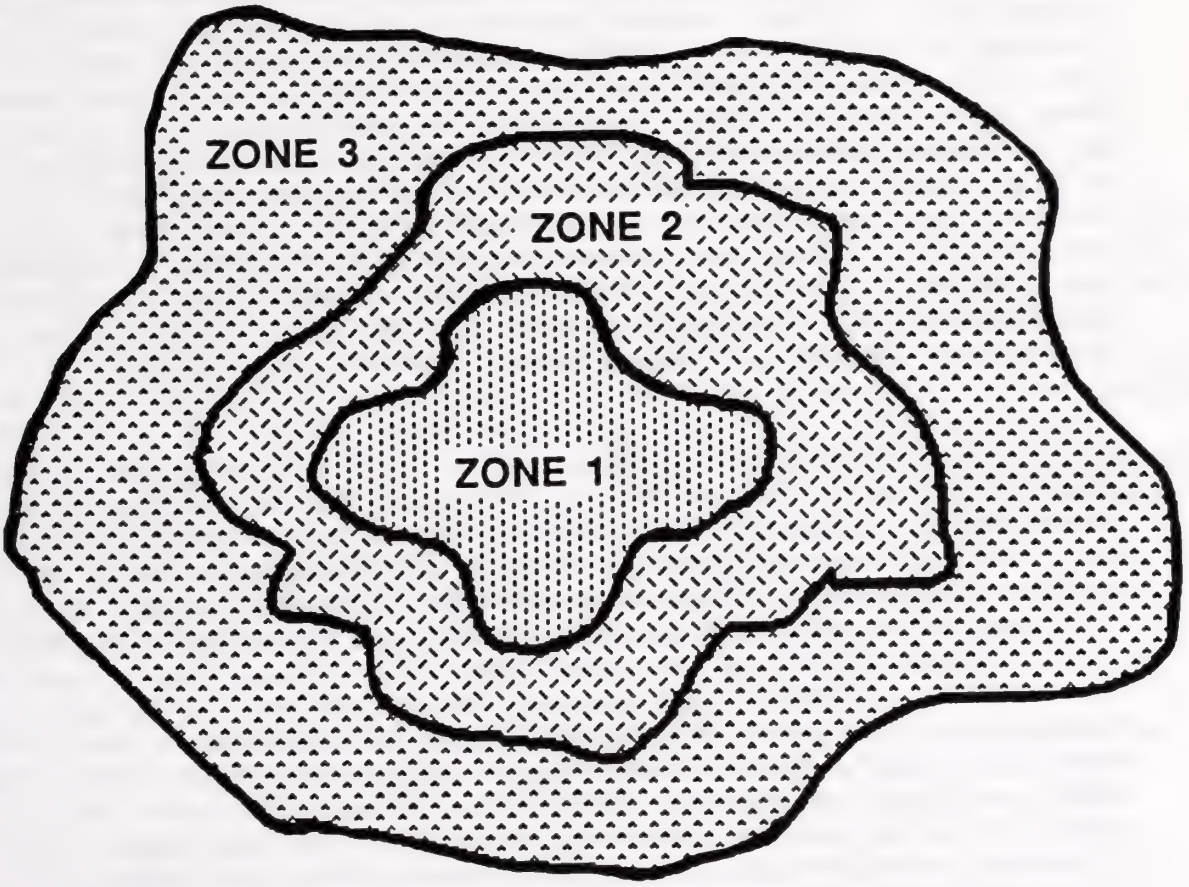


Fig. 6. Basic zone management concept for wolves in the GYA.

Zone management of wolves has increased in popularity recently in Canada and Alaska. Several agencies have zone management systems in the planning stage. These are described primarily in internal documents, and little implementation has occurred to date. Limited zone management of wolves has been applied in Minnesota (50 CFR 17.40(d)), although not as recommended by the Eastern Timber Wolf Recovery Team (U.S. Fish and Wildlife Service 1978). Five management zones are recognized in that state, but the only meaningful difference in management exists between Zone 1 and Zones 2, 3, 4, and 5. Control of wolves can occur in the event of significant depredations on lawfully present domestic animals in Zones 2, 3, 4, and 5. Management Zone 1, consisting of 4,488 square miles in the northeast corner of Minnesota, was set aside as a sanctuary because it is important as wolf habitat, relatively undeveloped, few people live there, and the potential for conflicts with humans is minimal. No wolf control occurs there. The only type of conflict that has emerged in Zone 1 is depredations on dogs. The Eastern Timber Wolf Recovery Team proposed a regulated take in some areas of Minnesota, particularly Zone 4, but the take has never occurred. No taking for purposes of ungulate management occurs in Minnesota.

In the GYA, the area of greatest priority for wolves is Yellowstone National Park. Most discussions of a reintroduction and wolf recovery in the area have focused on the park itself. However, the park boundary is not a biologically meaningful boundary, and there is no guarantee that management priority (complete or near-complete legal protection) for wolves in the park alone would be adequate to allow a secure population to develop and persist over time. Although wolves have sustained themselves for decades in areas much smaller than Yellowstone National Park, e.g., Isle Royale and Riding Mountain National Parks, they have not had to contend with prey migration in those areas. The designated wildernesses and national forests outside of Yellowstone provide a buffer -- although an imperfect one -- between the park and most economic interests in the area that wolves might affect. Thus, the GYA may be particularly well suited to some geographically defined management zone system using three or more zones. The most obvious zone scenario would include management within the "buffer" area (Zone 2, Fig. 6) that is intermediate between that within the park and that farther from the park.

When zones are defined, consideration will have to be given to whether administrative, physiographic, or biological lines (or some combination of these) should be used. Major factors are to be considered in defining zones are: size of area necessary (and type of management therein) to support a viable wolf population, distribution and seasonal movements of prey, distribution of livestock allotments, and distribution of areas of potential conflict with state ungulate management objectives. The possibility exists that some wolves would move outside the park in winter following their prey. Potentially, some packs could follow prey to lower elevations in winter and establish dens in lower elevations, and thus not return to the summer ranges of their prey until midsummer. Careful attention would have to be given to the number of zones. Fewer zones may mean simplified management and increased ease of understanding for the public and agency personnel (Weaver pers. comm.) but less fine-tuning of management. Another consideration in defining zones is whether wolves should be protected over a greater area during the period of population establishment but limited to a smaller area after full recovery when more is understood about the biological requirements and behavior of wolves in the GYA. From the standpoint of wolf reestablishment, the highest priority should be given to provision of sufficient year-round resources to support a viable population of wolves. Although the definition of a viable population is debatable (Conner 1988), an effort to restore wolves to the GYA is improvident if that objective is not achieved.

When considering management and management zones for wolves, we must also consider who would be authorized to engage in the control of wolves. In previewing this question as it relates to the GYA, a broad range of possibilities can be envisioned, similar to the continuum (Fig. 5) for intensive control. Five distinct "who scenarios," going from less control to more control are:

1. No one is authorized to engage in control activities, except perhaps for government officials in the event of disease, threats to human life/safety, and nuisance behavior.

2. Control by state/federal officials only.

3. Control by state/federal officials and private landowners.

4. Control by state/federal officials and private landowners and by the public via a regulated harvest.

5. No restriction on who can control wolves.

The following section identifies five of the more obvious management zone scenarios from the numerous possibilities that exist for wolves in the GYA. Some of the possible variations of each scenario are discussed, and the impacts of each scenario are presented in the form of biological and administrative/socioeconomic advantages and disadvantages. Each scenario assumes that wolves would be introduced to Yellowstone Park as a nonessential experimental population, and that outside Zone 1 wolves would be managed by the states of Montana, Wyoming, and Idaho under a well-conceived conservation plan developed in concert with the federal agencies. Note that these scenarios use administrative boundaries while trying to emphasize the biological requirements of the wolf. Other approaches may be equally or more valid. Each scenario is described using the following standard terms which should be understood in context with the zone management concept (Fig. 6). Also note that these definitions and/or terms could change under a NEPA-type process and/or in development of special regulations for an experimental population.

Zone 1 -- Geographic area at center of the GYA of sufficient size and prey base to meet biological requirements of wolves and ensure survival and recovery (10 breeding pairs). Wolves would be almost totally protected within the zone. No control would occur in Yellowstone National Park except for occasional taking of nuisance or injured animals by park personnel. Wolves occurring outside Yellowstone Park (if the zone extends outside the park) would be managed by the states of Idaho, Montana, and Wyoming. (Note that in this discussion, Zone 1 is defined as a area in which no taking of wolves occurs for controlling livestock depredations or predation on big game species. However, there is no reason that such taking could not be permitted in Zone 1 if the taking was designed and regulated to be consistent with recovery goals.)

Zone 2 -- Area generally surrounding Zone 1 that may be important to the wolf population as a buffer zone between Zones 1 and 3. A moderate degree of protection for the wolf in this zone would enhance recovery objectives in Zone 1. The emphasis of wolf management would focus on state big game management objectives and wolf/livestock conflict resolution. Wolves would be managed by the states of Idaho, Montana, and Wyoming under a conservation plan consistent with the survival of the species, and wolves would be controlled only in response to confirmed depredations on domestic animals or intensive predation on ungulates and only by state/federal officials.

Zone 3 -- Area generally outside Zone 2 considered not vital to recovery of wolves and containing a level of human activity to cause

management of conflicts to be a major priority. Wolf management would focus on prevention of conflicts with livestock/ungulate management objectives. Wolf numbers and distribution would be managed by the states of Idaho, Montana, and Wyoming under a conservation plan consistent with the long-term survival of the species. The plan could include a regulated harvest and provisions for the public to take wolves on private and, possibly, public lands after documentation of depredations on livestock. Taking by state/federal officials would also be authorized.

Other outer zones could be described, e.g., Zone 4 where wolves would not be allowed. However, more than three zones would likely lead to unnecessary confusion. The outermost zone will, in effect, define the population and represent the outer extent of the area in which management under the experimental population rule can occur. Consequently, delineation of that zone would warrant greater attention than if a nonexperimental population was involved.

Management/Zone Scenarios

The following section presents five alternatives chosen from points along the continuum (Fig. 5) and incorporating the extremes of the continuum. Again, the scenarios presented below are intended to demonstrate how control and management activities might be set up. They describe the advantages, disadvantages, strengths, and weaknesses of different scenarios and illustrate the complexity inherent in wolf management in the GYA. The order in which these scenarios are presented is in no way indicative of preference. These scenarios do not represent choices or preferences of the FWS, the NPS, or any other state or federal agency.

Management/Zone Scenario 1

Zone 1 = Yellowstone National Park
No Zone 2
Zone 3 = All GYA lands outside of Yellowstone National Park (still to be defined)

Wolves would be reintroduced into Yellowstone National Park and totally protected inside the park except that taking by park personnel could occur under extraordinary circumstances such as disease, threats to human life, and nuisance behavior. Outside the park, management would be conducted by the states. Management regulations, written into special rules for the experimental population, would place few restrictions on taking by the public outside the park boundary (Fig. 1). Taking by state/federal officials would occur outside the park in response to depredations on livestock and to predation on ungulate species -- as deemed necessary by the agencies.

Advantages

Biological:

- Wolves might be able to occupy some areas outside Zone 1/outside park boundaries despite lack of protection there.
- Meets Zone 1 criteria in recovery plan.

Administrative/Socioeconomic:

- Simplicity; would make management of wolves straightforward and lines easy to learn.
- Most likely to have the support of parties most apprehensive about wolf reintroduction.
- Minimal conflict with livestock production on national forest allotments, other public lands, and private lands.
- Minimal conflict with ungulate management outside park.
- Gives states large role in wolf management/recovery.

Disadvantages

Biological:

- Uses administrative lines rather than biologically meaningful lines.
- Greatest mortality risk to Yellowstone National Park wolves.
- Neglects the concept of ecosystem management.
- No assurance that park alone provides enough space for viable population.
- Much of the park's prey migrates out of park in the fall and spends only about 150 days/year within the boundaries. If some wolves were migratory in response to seasonal movements of their ungulate prey and spent time in and out of the park, they would be vulnerable to excessive taking.
- Wolf packs whose year-round territories were partly inside and partly outside the park would be vulnerable to taking.

- Defines only about 19% of the greater Yellowstone area as a wolf recovery area, leaving other suitable areas not utilized as such.

- Longer time to recovery and delisting than with Scenarios 2, 3, 4, and 5 (unless 10 pairs first colonize the park).

Administrative/Socioeconomic:

- High level of controversy due to wolves being harvested up to park boundary.

- Legal taking by public adjacent to park might encourage poaching just within park boundary; such a problem might be difficult to prevent from law enforcement standpoint.

- Least acceptable of alternatives to most organized proponents of wolf reintroduction.

- May still allow an increase in depredation on livestock in the area (above current level).

- The extent of public taking of an experimental population included in this option probably would be more difficult to justify and implement than the taking described in Scenarios 2, 3, 4, and 5, as taking must be consistent with the long-term conservation of the species.

Scenario 1 provides perhaps the most modest picture of wolf recovery imaginable for the GYA because wolves are protected only within Yellowstone National Park. It is the scenario with the least expected impact on livestock and big game hunting. The most serious potential shortcoming of this scenario is that it might not provide enough space and protection for wolves to allow them to ever reach recovery level in the GYA which would delay delisting indefinitely. Because so much of wolves' prey migrates out of the park in winter, it is unclear how much area and which areas wolves would need to reach recovery level.

A potential variation of Scenario 1 would be to allow problem wolves to be controlled within the park when they are known to be problem individuals. Another possible variation would be to provide protection for those wolf packs that have home ranges primarily within the park while they are outside the park. This might be difficult to enforce, however, and such ranges probably would not be static from year to year, thus causing frequent redescription and/or refinement of the area of wolf protection.

Management/Zone Scenario 2

Zone 1 = Yellowstone National Park
Zone 2 = Designated wilderness adjacent to Yellowstone National Park
Zone 3 = All other GYA lands (still to be defined)

Wolves would be reintroduced into Yellowstone National Park. No control would occur within the park except that taking could occur by park personnel in the event of disease, threats to human life, and nuisance behavior (as in Scenario 1). Control by state/federal officials would be permissible within designated wilderness in response to confirmed depredations on livestock and to excessive predation on big game species that conflicts with state management objectives (Fig. 2). No taking by the public would be permitted inside designated wilderness areas. Outside designated wilderness (i.e., in Zone 3), taking by state/federal officials would be permissible in the same circumstances as above and regulated public harvest.

Advantages

Biological:

- Allows more space than just the park, probably reducing risk to the wolf population (assuming few wolves would need to be taken in wilderness areas) and reducing time to recovery compared to Scenario 1.
- Allows wolves to utilize the Gallatin, the Clarks Fork, and the North Fork Shoshone elk herds on their winter ranges.
- More command over control activities than in Scenario 1 by requiring work by federal or state designees in wilderness areas.
- Higher probability that wolves taken near the park would be offending wolves than in Scenario 1.

Administrative/Socioeconomic:

- Control by state/federal officials within wildernesses rather than by the public may be more acceptable to the conservation community.
- Effectively separates area of maximum wolf protection from areas with greatest density of livestock allotments.

Disadvantages

Biological:

- Longer period necessary to reach recovery than with Scenarios 3, 4, and 5.
- Designated wilderness boundaries are not the same as wintering herd boundaries.
- Would allow wolves to exploit the Gallatin elk herd (already harvested at or near maximum sustained yield) and the Jackson elk herd.

Administrative/Socioeconomic:

- Wilderness areas (Zone 2) would still take in a number of livestock allotments.
- Raises questions of how to manage wolves in isolated wildernesses.
- Additional workload could strain capability of agencies to conduct control of coyotes and other predators.

Scenario 2 affords slightly more protection for the wolf than Scenario 1 by precluding public taking of wolves in the designated wildernesses around Yellowstone National Park. Wolves would still be taken in cases of depredations on livestock and in cases of excessive predation on ungulates, but the taking would be limited by site and duration and might have only minor impact on the wolf population. Requiring such control activities to be by state/federal officials and excluding the public in Zone 2 might further limit the effects on wolves while still solving conflicts.

Variations and/or exceptions to Scenario 2 could be inclusion of some wildernesses and exclusion of others in Zone 2. For example, some wildernesses or portions thereof could be in Zone 1 and others in Zone 3, thereby tailoring the degree of wolf protection to specific circumstances. Another logical alternative would be for the states to allow unregulated taking in Zone 3 instead of allowing a regulated harvest.

Management/Zone Scenario 3

Zone 1 = Yellowstone National Park
Zone 2 = All other public GYA lands
Zone 3 = All privately owned lands

Wolves would be reintroduced into Yellowstone National Park and managed within the park as described in Scenarios 1 and 2 above, i.e., no control would occur within the park except that taking could occur by park personnel in the event of disease, threats to human life, and nuisance behavior. Control by state/federal officials would be permissible on wilderness and all other public GYA lands outside the park in response to depredations on livestock and to excessive predation on ungulate species that conflicts with state management objectives. Taking by the public would be permissible on private lands in response to livestock depredations, but anyone killing a wolf would have to demonstrate that a depredation had occurred.

Advantages

Biological:

- Considerable space and protection made available to wolf population, probably reducing risk to wolves and reducing time to recovery compared to time for recovery in Scenario 1 and 2.
- Latitude to take wolves on private land will go far to mollify local public without loss of many wolves and with minimal impact on conservation of species. Illegal killing might be reduced.
- Wolves taken on federal lands and private lands likely to be depredators because of site-specific and time-specific nature of control actions.

Administrative/Socioeconomic:

- The need to take wolves in wilderness may be low.
- Taking by livestock owners on private land in response to depredations is consistent with recommendations of the recovery team.

Disadvantages

Biological:

- Longer time required to reach recovery than with Scenarios 4 and 5.

Administrative/Socioeconomic:

- Possible maximum need for state and/or federal control actions because of exclusion of public on public lands; could strain those agencies.
- Taking by the public unlikely to be supported by conservation community.
- Taking by the public on private land would be difficult to regulate from an enforcement perspective.

Scenario 3 offers even more protection to the wolf than Scenarios 1 and 2 by disallowing the public from taking wolves on all government-owned lands within the GYA. The public would still be allowed to take wolves that prey on livestock on privately-owned land. Control by state/federal officials would still be permissible on public lands outside the park as well as on privately-owned lands.

A variation of this scenario would be to allow the public to take wolves anywhere in Zone 3 without restrictions. Another variation would be to allow a regulated take by members of the public in Zone 3. Either option probably could occur with minimal ill effects on the wolf population and might serve to help contain the experimental population. Still another of the possible variations of Scenario 3 is to involve the public in a closely regulated take of wolves within Zone 2 that is designed to reduce wolf numbers in areas of chronic livestock depredations and areas of intensive predation on big game herds.

Management/Zone Scenario 4

Zone 1 = Yellowstone National Park plus adjacent wilderness
Zone 2 = All other GYA lands (still to be defined)
No Zone 3

Wolves would be reintroduced into Yellowstone National Park and managed within the park as described in Scenarios 1, 2, and 3 above. No control of wolves would occur within the park or within wildernesses. Control by state/federal officials would be permissible on all other GYA lands in response to depredations on livestock or excessive predation on ungulate species that conflicts with state management objectives. There would be no taking by the public on either public or private land.

Advantages

Biological:

- Increases area of total wolf protection by 169% (3,754,100 acres) beyond Yellowstone National Park alone.
- Might allow population to reach recovery faster and be more secure than would be possible under Scenarios 1, 2, and 3.

Administrative/Socioeconomic:

- Consistent with wilderness concept.
- Provides more space for wolves to take advantage of the selected herds.
- Encompasses small percentage of grazing allotments on national forests.

Disadvantages

Biological:

- Uses administrative boundaries rather than biological boundaries; may or may not be providing the biological resources necessary for wolf recovery.
- No provision made for wolves to follow elk herds on south and southwest sides of the park to their winter range.

Administrative/Socioeconomic:

- Precludes control actions on some grazing leases.
- Allows the possibility of overexploitation of ungulate populations in wildernesses without the option of wolf control.
- Presents opportunity for wolves to exploit moose, a highly prized big game species.
- Predation on ungulates may affect hunter opportunity.
- Would alienate some outfitters because wolves will be protected in their assigned hunting areas.

- Livestock industry likely to oppose because public control of wolves would be prohibited (even on public land).

- Places severe restrictions on the extent to which states can manage wolves and thus might discourage state participation in wolf management/recovery.

This scenario gives the wolf still more legal protection than in Scenarios 1, 2, and 3 by expanding the area of near complete protection from Yellowstone National Park to the park plus adjacent wildernesses. Being legally protected over this larger area might make a substantial difference in the ability of a wolf population to become established and reach a viable level in the GYA, one reason being that wolf packs could utilize migratory prey outside the park (in most areas at least) without being vulnerable to excessive take when they leave the park. This scenario does not resolve the question of how to deal with killing of livestock and excessive predation on big game within wilderness areas in conflict with big game management objectives.

A variation of the scenario would be to allow designated state/federal officials to take wolves within wildernesses in response to livestock depredations, with requirements limiting the taking to the immediate vicinity of the stock loss (or otherwise maximizing the chances that any wolf (wolves) taken was (were) the offending wolf (wolves)). Such limited control could be specifically designed and regulated to meet the recovery goal of 10 packs. Similarly, control of wolves to reduce local excessive predation on game herds could occur in limited circumstances. This approach would essentially redefine Zone 1, as defined above, to provide for limited taking outside Yellowstone National Park. There is no reason that limited control could not be allowed in the area designated as Zone 1. Problem wolves could be relocated rather than killed in these circumstances to reduce the impact on viability of the wolf population. Another variation of this scenario would be to have a Zone 3 that was defined as all privately owned lands within the GYA and possibly including public lands outside some defined area and have a state-regulated take of wolves in Zone 3.

Management/Zone Scenario 5

Zone 1 = All GYA lands (perimeter must be defined distinctively)
No Zone 2
No Zone 3

Wolves would be reintroduced into Yellowstone National Park and managed within the park as described in Scenarios 1, 2, 3, and 4 above. No control of wolves would be allowed throughout areas described for the experimental population in rulemaking, regardless of circumstances (exceptions for defense of human life and other standard reasons normally allowed with listed species). No control actions would be conducted by state or federal agencies in the park or any GYA lands in response to depredations on livestock or excessive predation on ungulate herds. No taking by the public would be allowed on public or private lands.

Advantages

Biological:

- Maximum opportunity for wolves to thrive and reach delisting level as soon as possible.
- Increases area of wolf protection by about 529% (beyond the park).
- Alleviates the potential problem of prey migrating outside the range of the wolves in winter.
- Increases number of elk available to wolves by some 560% to roughly 93,000.
- Might allow utilization of the diversity of prey in the ecosystem; lessens reliance on elk. Dramatically increases availability of mule deer to wolves.
- Minimizes human-caused mortality (legal), thereby allowing natural factors to regulate population. Wolf population most secure, most resistant to extinction.

Administrative/Socioeconomic:

- Wolves may disperse into and live within many national forests, with little conflict anyway.
- Possibility of little effect on GYA's elk herds; most are increasing.
- Shortest time to recovery and delisting.

Disadvantages

Biological:

- Illegal killing of wolves may be high because of public resentment over protected status throughout the GYA.

Administrative/Socioeconomic:

- Probably highly objectionable to local public.

- Public resentment might spill over to other endangered species in the area to the detriment of these and other wildlife conservation programs.

- States might be unwilling to participate in management of wolves under such restrictive terms.

- Maximum potential for depredations on livestock on public and private lands, and no effective means of dealing with depredations on livestock.

- Without removal of problem wolves from population, level of depredation on domestic animals will increase over the long term.

- Maximum potential for conflicts with state ungulate management objectives and hunter opportunity; protects wolves over an area important for hunting: annual number of hunter days = 20,999,160 (21,693,560 planned).

- Presents opportunity for wolves to exploit moose, a highly-sought game species.

- Fails to take advantage of flexibility in the experimental population designation.

- May conflict with criteria used in recovery plan for selecting recovery areas.

- Wolves could not be controlled in Grand Teton National Park and National Elk Refuge, thereby exacerbating certain management problems.

- With Grand Teton Park included in recovery area, Section 7 would be invoked inside park raising questions about a limited harvest of elk authorized by state of Wyoming.

Scenario 5 provides the most conceivable protection to wolves in the GYA recovery area. This alternative is most favorable to the wolf in terms of survival of transplants, establishment of a viable population, and increase of that population to such a level that the risk of extinction is minimal. On the other hand, Scenario 5 provides the least opportunity to deal with conflict situations that will arise. The scope of those conflicts under this option might well result in a level of animosity and illegal killing that would offset the advantages to wolves that the option would attempt to provide.

Several variations to Scenario 5 could be imagined. One variation would be to allow state/federal officials to exercise wolf control only on private land or nonfederal land. Another variation would be to allow a small degree of control but limit the control to nonlethal methods.

Other Management/Zone Scenarios

In addition to the five management/zone scenarios that have been described above, there are two options of a different type that deserve brief mention. (These were not included above because they do not fit the "continuum model" as well as Scenarios 1 through 5 fit that model.) One option would provide complete protection for wolves within an area that includes the park plus winter ranges of selected migratory elk herds that summer in the park (Fig. 3). This approach would solve the potential problem of wolves following the elk that winter outside the park; a question that cannot be answered until wolves are living in the park. The outward boundary of Zone 1 (complete protection) could flex seasonally to encompass some of the migrating herds. A major consideration of this scenario is that, on the southwest and west sides of the park, Zone 1 would have to extend for several miles to encompass all of the winter range of the migratory elk herds there. If wolves were completely protected there, conflicts with cattle and sheep production could occur, especially where ungulates winter with or next to livestock (as on private land). Such a zone that would flex with elk migrations might include Grand Teton National Park and the National Elk Refuge for a large part of the year, thereby invoking full Section 7 consultation requirements. This might jeopardize the limited elk harvest authorized by the state of Wyoming in Grand Teton National Park to help manage the increasing Jackson herd. Wyoming has expressed opposition to protection for the wolf in Grand Teton National Park and in the area south of the Buffalo Fork of the Snake River east of the park. The potential problems in applying the management/zone scenario described illustrate that exceptions to general approaches may have to be made to obtain endorsement of any general management/zone concept.

A second alternative management/zone scenario, aside from the five scenarios on the control continuum, could be fashioned after management of the grizzly bear in the GYA (Fig. 7). Grizzly bear habitat is described by different management situations (MS), with three situations described in the GYA based on habitat components, bear use and presence, and other uses or activities (Greater Yellowstone Coordinating Committee 1987:3-133). In MS-I, grizzly habitat and its improvement receive the highest management priority and management decisions favor the bear when grizzly habitat and other uses compete. In MS-II, the bear is accommodated, if feasible, but not to the exclusion of other uses, and in MS-III, management decisions do not consider habitat maintenance and improvement and stress minimizing grizzly-human conflicts. This model yields at least two wolf management/zone options. First, Zone 1 could be equivalent to MS-I; Zone 2 could be the equivalent of MS-II, and Zone 3 could be the equivalent of MS-III and all other remaining GYA lands. This scenario would bring the area in which wolves receive complete protection to 4,094,700 acres (6,398 square miles). The extension of the area of total protection beyond most of the park boundary would add a significant amount of elk winter range and add to the vitality of a wolf population.

GREATER YELLOWSTONE AREA
LEGEND
Management Situation I
Management Situation II
Management Situation III
Map Note: In Grand Teton National Park and John D Rockefeller Jr Memorial Parkway Management Situation III Habitat includes all developed areas, private land and an area 250 yards adjacent to all paved roads.

Such a scenario with total protection beyond the park in some areas, the opportunity for control by state/federal officials within a "buffer" zone of sorts, and state management with public involvement still farther away from the most critical wolf area may offer a reasonable compromise that could well serve all interests. Control for livestock depredations could be allowed in the portion of MS-I outside the park (state/federal officials) probably with little impact on the wolf population.

The most obvious variation of the above would be to have Zone 1 be the equivalent of MS-I and MS-II combined. This would be more favorable to the wolf by bringing the area of total protection to 9,304 square miles and further increase availability of wintering migratory elk and other ungulates. Land ownership in the area would be 99% federal and only 1% private. The management lines are already familiar to agency personnel. Some possible disadvantages and concerns surrounding this scenario include the following: 1) habitat needs of the wolf are not the same as those of the bear, 2) the MS boundaries do not necessarily include winter ranges of elk (they were not necessarily drawn with that in mind), 3) the boundaries allow greater utilization of the North Fork Shoshone elk herd which is decreasing and the Gallatin elk herd which is harvested at near maximum sustained yield, 4) the boundaries include considerable moose summer and winter range, 5) the boundaries include bighorn sheep summer and winter range in Wyoming, especially if MS-II is included, and 6) part or all of Grand Teton National Park would be included raising problems with elk harvest there.

In summary, an array of options for wolf control and management zones are available for the GYA. Several options have been described above, and many variations and/or additional scenarios could have been described. Rather than recommend a control strategy and zone system, the objective here has been to present a range of scenarios extending from extensive control to little or no control. With progressively more control, the potential for conflicts decreases, but the risk to the wolf population increases, time to recovery and delisting increases, and the likelihood of reaching recovery level (10 breeding pairs) decreases. Conversely, with less control, the potential for conflicts increases, but the risk to the wolf population decreases, time to recovery and delisting decreases, and the likelihood of reaching recovery increases. Each scenario presented here offers certain advantages and disadvantages depending upon the priority under consideration. Each of the scenarios presented could have many variations to accommodate special concerns. Because so many possibilities are available, it would seem that the opportunity exists to reach agreement on a management arrangement that would satisfy the biological needs of the wolf and allow recovery and delisting while satisfying the vast majority of concerns of most interested parties. Public input may be extremely beneficial on these issues. More complete agency and public involvement could be very advantageous in fully defining control options and management zones.

Fig. 7. Grizzly bear management zones in the GYA.

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SECTION 2

The Prey Base for Wolves in Yellowstone National Park

THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK I: Five Species on the Northern Range, Elk Parkwide

Francis J. Singer
National Park Service
Division of Research
P.O. Box 168
Yellowstone National Park, WY 82190

THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK I: Five Species on the Northern Range, Elk Parkwide

Francis J. Singer, National Park Service, Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190

EXECUTIVE SUMMARY

1. Population and harvest data from the 1980's are presented for eight ungulate species that occur in Yellowstone National Park: bighorn sheep (Ovis canadensis) bison (Bison bison), elk (Cervus elaphus), mule deer (Odocoileus hemionus), moose (Alces alces), mountain goat (Oreamnos americanus) pronghorn (Antilocapra americana), and white-tailed deer (Odocoileus virginianus). Five of these ungulates, elk, mule deer, moose, white-tailed deer and pronghorn utilize Yellowstone's northern range. Data are also presented for the eight elk herds that winter, summer, or reside year-round within the park boundary including the Clarks Fork, North Fork Shoshone, Carter Mountain, Jackson, Sand Creek, Gallatin, and Madison-Firehole herds.

2. During the period 1980-1988, an average of about 17,457 (range of counts 10,226-19,000) elk wintered on Yellowstone's northern range, and about 1,900 elk wintered on three other ranges within Yellowstone National Park. Mule deer counts averaged 1,914 (1,007-2,274), pronghorn 392 (102-495), bison 433 (233-594), and bighorn sheep 195 (218-607) on the northern winter range. A minimally recovered wolf population of 10 pairs of about 100 wolves would correspond to the following mean ratios for the 1980-1988 period: 1) 1 wolf:145 ungulates on the northern winter range within the park (14,491 ungulates), 2) 1 wolf:231 ungulates for all of the northern winter range and all other park winter ranges combined (23,085 ungulates), and 3) 1 wolf:186 ungulates for all of the northern range both inside and outside Yellowstone National Park (18,555 ungulates).

3. During the period 1980-1988, the eight species of ungulates occupying Yellowstone National Park during summer exceeded 37,804 individuals. A mean estimated 31,136 elk from eight herds spent the summer within the park. Summering elk spent an average of 138-160 days in the park, or about 38%-43% of the year. A minimally-recovered wolf population of 10 pairs or about 100 wolves would correspond to the following mean ratios for the 1980-1988 period: 1 wolf:378 ungulates during summer parkwide (37,804 ungulates). Wolf to ungulate ratios ranged from 1 wolf:96 to 1 wolf:328 ungulates in seven wolf-occupied areas elsewhere in North America. Yellowstone's summer ungulate numbers are underestimated since an unknown additional number of mule deer and moose migrate into the park each summer. Hunters also utilize the ungulate prey base, as do other predators within Yellowstone Park. These predators include grizzly bears (Ursus arctos),

black bears (Ursus americanus), coyotes (Canis latrans), and mountain lions (Felis concolor). Wolf to ungulate ratios should be used for preliminary estimates only because of:

1) functional responses of wolves to changes in prey densities,

2) lags in numerical responses of wolves,

3) the role of buffer prey species, and

4) differences due to the proximity of the ungulate population to its nutrient-climate ceiling.

4. The 1988 drought reduced plant biomass and caused early plant senescence, while the 1988 fires burned portions of winter ranges in the fall. Several arctic storm fronts exacerbated winter severity. As a result, during the winter of 1988-1989, many ungulates were winterkilled and the late season harvest of elk increased. Due to both of these factors, elk population estimates for the northern winter range declined 40%; mule deer counts declined 21%, and pronghorn counts declined 25%. Recovery to at least prefire levels is necessary before gray wolves (Canis lupus) could be restored to Yellowstone.

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THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK I:

Five species of ungulates on the northern Yellowstone elk winter range, elk parkwide.[1]

Francis J. Singer, P.O. Box 168, Yellowstone National Park, WY 82190

ABSTRACT: Data was gathered on numbers, productivity, and harvest levels for eight ungulate species that occur in Yellowstone National Park: bighorn sheep (Ovis canadensis) bison (Bison bison), elk (Cervus elaphus), mule deer (Odocoileus hemionus), moose (Alces alces), mountain goat (Oreamnos americanus) pronghorn (Antilocapra americana), and white-tailed deer (Odocoileus virginianus). The present analysis includes five species that occur on the northern range including eight elk herd units parkwide. During the period 1980-1988, an average of 17,457 (10,226-19,000) elk, 433 (233-594) bison, 392 (102-495) pronghorn, a range of 195 (218-607) bighorn sheep, and 1,814 (1,004-2,274) mule deer were counted on the northern range. Average ungulate ratios on the northern range during the 1980's were 100 elk:10 mule deer:2 bison:2 pronghorn: 1 bighorn sheep: 1 moose. Due to a severe drought, burning of winter ranges, and severe winter conditions in 1988-1989, elk numbers declined about 40%, mule deer about 21%, and pronghorn about 25%. All eight ungulate species available to gray wolves (Canis lupus) in summer exceeded 37,804 and in winter exceeded 23,085, 1980-1988. Immediately postfire in 1989, total ungulate numbers were reduced to about 18,098 ungulates in winter. Grizzly bears (Ursus arctos), black bears (U. americanus), coyotes (Canis latrans), and mountain lions (Felis concolor) also occupy the park and also kill ungulates. Average wolf to ungulate ratios, 1980-1988, for 100 wolves would have been:

1) 1 wolf:145 ungulates on the northern elk winter range within the park boundary only (average 14,491 ungulates)

2) 1 wolf:186 ungulates for all of the northern range, both inside and outside of the park boundary (average 18,555 ungulates)

3) 1 wolf:231 ungulates for all park winter ranges combined (average 23,085 ungulates)

4) 1 wolf:378 ungulates during summer parkwide (average 37,804 ungulates).

Wolf to ungulate ratios are useful for preliminary assessments because of responses by wolves, wolf use of nonungulate prey during summer, and the variable vulnerability of ungulates in relation to their respective proximity to ecological carrying capacity -- the ungulate's nutrient-climate ceiling.

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[1]Manuscript accepted for publication in Examining the Greater Yellowstone Ecosystem.

Yellowstone National Park was identified as one of three potential recovery sites for the gray wolf (Canis lupus) (U.S. Fish and Wildl. Serv. 1987). Many questions have arisen regarding the prospect of Yellowstone National Park and surrounding areas serving as a successful recovery site. On the one hand, large, generally unhunted populations of elk (Cervus elaphus) and bison (Bison bison) exist in the area, the size of remote national park and forest wilderness areas exceeds five million acres, and the wolf is the only missing element of Yellowstone's fauna. On the other hand, big game hunting is a major industry in the greater Yellowstone area, and the extent to which wolves will populate areas outside of the park and compete with hunters for elk and other ungulates is unknown. Contentions range from no effect of wolves on big game at all to minor impacts (Fischer 1986) to significant effects (Zumbo 1987).

Ungulates comprise the bulk of the wolf's diet across North America (Mech 1970). A first step in determining the potential success of wolf reintroduction to the Yellowstone area is to gather and consolidate information on the park's ungulate herds. Eight elk herds summer within Yellowstone National Park (Houston 1982:33), but only four elk herds winter wholly or partially within the park. Three bison herds exist within the park (Meagher 1973). Two of these bison herds, the Pelican Valley and Mary Mountain herds, occupy areas with deep winter snows on the park's Central Plateau (Meagher 1971). Mule deer (Odocoileus hemionus) summer throughout the park, but most leave the park in winter because of deep snows. Bighorn sheep (Ovis canadensis) winter in eight locales on the northern range (Houston 1982:161). Moose (Alces alces) are found in low numbers throughout the park in summer and winter. Pronghorn (Antilocapra americana) winter in a restricted area of the northern range near Gardiner, Montana. Some pronghorn migrate each summer to the Lamar Valley, Tower Falls, and Gardners Hole areas of the northern range. A few white-tailed deer (Odocoileus virginianus) are observed throughout the park each summer.

This paper primarily discusses the five ungulate species inhabiting the northern winter range. This area holds the greatest prospects for year-round wolf occupation, since it is the winter range for the greater Yellowstone area's largest ungulate prey base. Parkwide data on elk numbers and demography are also presented since elk are by far the most numerous ungulate in the park area. Greater detail on bison and bighorn sheep are presented elsewhere (Meagher 1973, 1989; M. Meagher, Natl. Park Serv., pers. comm.).

DESCRIPTION OF STUDY AREAS

Yellowstone National Park

Nearly the entire area of Yellowstone National Park provides summer range for elk and to some extent other ungulates. The park is 79% forested, about 81% of this forest is dominated by lodgepole pine (Pinus contorta) at elevations between 2,300 m and 2,600 m (Houston 1982). In summer, elk are concentrated near wet meadows, herblands on the higher plateaus, alpine tundra, and a wide variety of forest openings (Meagher 1973, Houston 1982).

Winter snowfalls force elk and other ungulates to leave the majority of the park area. For example, annual precipitation on the Pitchstone Plateau is 190 cm, most of which falls as snow, while other high plateaus and ridges (Two Ocean Plateau, Big Game Ridge, Chicken Ridge) receive nearly as much snowfall.

Northern Winter Range

Houston (1982) described Yellowstone's northern winter range as about 100,000 ha between Silver Gate and Dome Mountain, Montana, where the northern Yellowstone elk herd spend their winters. About 82% of the northern winter range lies within Yellowstone National Park, and the remaining 18% lies north of the park boundary on Gallatin National Forest and private lands. Northern range elevations are lower (1,500-2,400 m) and somewhat warmer, receiving less precipitation than the rest of the park (Houston 1982); thus, more ungulates are able to winter in the area than on the park interior's higher plateaus (Meagher 1973, Houston 1982). Most of the northern range averages 75 cm or less of total precipitation (Houston 1982; P. Farnes, Soil Conserv. Serv., unpubl. data). Precipitation, however, varies greatly due to the considerable range in elevation. For example, mean annual precipitation is 30 cm near Gardiner, Montana, but 55 cm near the Lamar Ranger Station, 35 km farther uprange.

About 41% of the northern winter range is forested, largely Douglas-fir (Pseudotsuga menziesii) stands with a grass understory (Cooper 1975, Houston 1982, Despain in press). About 55% of the area is grassland, especially Idaho fescue (Festuca idahoensis) and big sagebrush (Artemesia tridentata) habitat types (Mueggler and Stewart 1980), about 2% aspen (Populus tremuloides) stands, and about 0.4% willow (Salix spp.) and riparian shrub stands. Most of the arable bottomland north of the park boundary consists of seeded and irrigated hayfields. These fields attract pronghorn, mule deer, and bison and are also used to a lesser extent by elk during severe winter weather.

METHODS

Yellowstone National Park

State agencies from Idaho, Montana, and Wyoming were contacted for data on elk herd counts, elk movements into the park, and elk harvest statistics from areas bordering the park. The relative proportion of elk migrating into Yellowstone National Park each summer was estimated from the proportion of animals who were radiocollared on winter ranges and who then migrated to Yellowstone (Cada 1975, Rudd 1982, Taylor 1986, B. Smith unpubl. data) combined with aerial summer range estimates (Brown 1985). Park files and survey reports for ungulate counts between 1980 and 1984 were reviewed. Counts and classifications of elk, mule deer, and moose were conducted from 1985 to 1988 in the park, and pronghorn monitoring was conducted from 1985 to 1987.

Northern Winter Range

Pronghorn. Aerial counts indicating minimum size of the pronghorn population were made from 1969 to 1989 using a small fixed-wing aircraft (Piper Super Cub). The counts were made at initial green-up, usually in March or early April, when pronghorn were still concentrated on winter range (1979-1989, Table 1). Two to three ground classifications of pronghorn sex and age groups were made during the same years. The counts and classifications through 1979 are provided in Houston (1982).

Moose. Moose were counted from Piper Super Cubs incidental to elk surveys by both Barmore (1980) and Houston (1982) for the period 1969-1978. Both researchers tallied moose over the entire northern range. The areas flown, flight patterns, and pilot were consistent during all of these years. Moose were not surveyed over the entire northern range after 1979. During the winters of 1985-1988, only the upper ends of five drainages (Soda Butte, Pebble, Slough, Buffalo Fork, and Hellroaring Creeks) on the northern range were flown. Five or six aerial surveys were flown during each winter-spring period. No sightability correction was available for moose.

Horseback surveys of moose were conducted in the upper ends of the same five drainages on the northern range outside of the park. These surveys were conducted during two periods, 1942-1949 and 1985-1987 (Swenson 1985, Puchlerz 1986). The same trails were ridden each year during mid-September. About 11-15 km were ridden each day, and the average number of moose seen per rider-day was tabulated.

Mule Deer. Mule deer were counted by one observer from a small helicopter in 1979, 1986, 1988, and 1989. In 1987, a Jet Ranger II helicopter and two observers were employed. Fawn:adult ratios were recorded during the helicopter surveys. These surveys were conducted during the period of spring green-up, usually from late February to late March. Areas surveyed, sequence of areas surveyed, and one observer (Singer) remained consistent between the surveys. No sightability correction was available for mule deer.

Elk. Elk were counted from a Piper Super Cub during a one- to three-day period in early winter for the period 1952-1979. Data from these and more variable aerial and ground counts are summarized through the year 1979 in Houston (1982). Two aircraft with pilot-observer teams were used to count elk in the winter of 1981-1982, but no more counts were made until 1985. During the next three winters, 1985-1988, elk counts were completed in a single day using four aircraft simultaneously to eliminate errors from elk movements between count days. No sightability correction was available for elk prior to 1986.

Table 1. Highest aerial counts of pronghorn on Yellowstone's northern range, 1979-1989.

Year	Number of Pronghorn	Pronghorn Per Square km	Date of Count	Observer/Pilot*
1979	152	3	4/16	M. Meagher/D. Stradley
1980	157	3	4/08	M. Meagher/D. Stradley
1981	102	2	3/21	M. Meagher/D. Stradley
1982	131	3	4/17	M. Meagher/D. Stradley
1983	310	6	3/08	M. Meagher/D. Stradley
1984	365	8	3/23	T. Black/D. Stradley
1985	364	8	4/09	A. Mitchell/D. Stradley
1986	363	8	2/28	F. Singer/B. Ferguson
1987	478	10	3/17	C. McClure/D. Stradley
1988	495	10	4/16	K. Buechner/B. Ferguson
1989	372	8	4/13	D. Trofka/B. Chapman

*All aircraft were Piper Super Cubs.

Table 2. Pronghorn damage control hunt statistics on Yellowstone's northern range, 1985-1989. Data obtained from K. Alt, Montana Department of Fish, Wildlife and Parks files.

Year	No. Permits Issued	No. Animals Killed	Approximate Percent of Herd
1985-1986	15	10-12	3
1986-1987	50	12-15	2
1987-1988	39	16	3
1988-1989	100	49	10

The elk counts after 1986 were subjected to sightability corrections according to the method of Samuel et al. (1987). A total of 47 elk were radiocollared on the northern range between 1986 and 1988. The northern range was divided into 66 count units (Fig. 1). Each count unit was flown in sequence by a pilot-observer team and the search time was recorded. From the air, each group of elk was counted, radiocollars were noted, the group location was plotted on a 1:24,000 scale map, and the percent snow cover and percent tree cover were estimated. Immediately before or after the survey flight, a separate aircraft was used to locate all radiocollared elk. A sightability model (stepwise logistic regression) employing the variables of pilot, observer, search time per square mile, percent tree cover, percent snow cover, and group size was developed from the numbers of radiocollared elk observed or not observed. The model was then applied to the conditions of tree cover, snow cover, and group size observed in each count unit during each survey (Samuel et al. 1987). All 66 count units were flown during each aircraft survey.

Classifications of elk sex and age groups were made from the park road with the aid of a 15-45 power spotting scope, 1964-1986 (Barmore 1980, Houston 1982, J. Swenson unpubl. data). During late winter in 1987, 1988, and 1989, classifications of elk sex and age were conducted from a helicopter.

RESULTS AND DISCUSSION

Pronghorn

Between 1930 and 1947, pronghorn numbers on the northern winter range varied from 500 to 800 (Houston 1982). Concern about declines in big sagebrush on the pronghorn winter range motivated park staff to artificially reduce pronghorn numbers during the 1947-1967 period (Houston 1982:168). As a result of the reductions, counts were below 200 during the 1969-1980 period (Scott 1987, Houston 1982). Fawn ratios remained low at 38 ± 15 (x ± S.D.) fawns per 100 does from 1967 to 1979 (Houston 1982). However, during the 1980's, pronghorn increased threefold to nearly 500 animals (Table 1). Fawn ratios were not determined from 1980 to 1984, but ratios after 1984 were higher than for the 1967-1979 period. A total of 80 fawns per 100 does was observed in November 1986, the highest recorded ratio since 1963 (Houston 1982). Pronghorn density on the 48 km area of winter use increased from 3 per km^2 in 1979 to 10 per km^2 in 1988. Pronghorn declined about 27% following the drought of 1988 and the severe winter of 1988-1989.

In 1983, owners of the Royal Teton Ranch plowed and reseeded two fields near Spring Creek, about 0.5 km north of the park, which attracted 20-25 pronghorn. After complaints from the landowner, a damage-control hunt was instituted on the ranch from 1985 to 1988 (Table 2). About 2%-10% of the total herd was harvested each year on private lands.

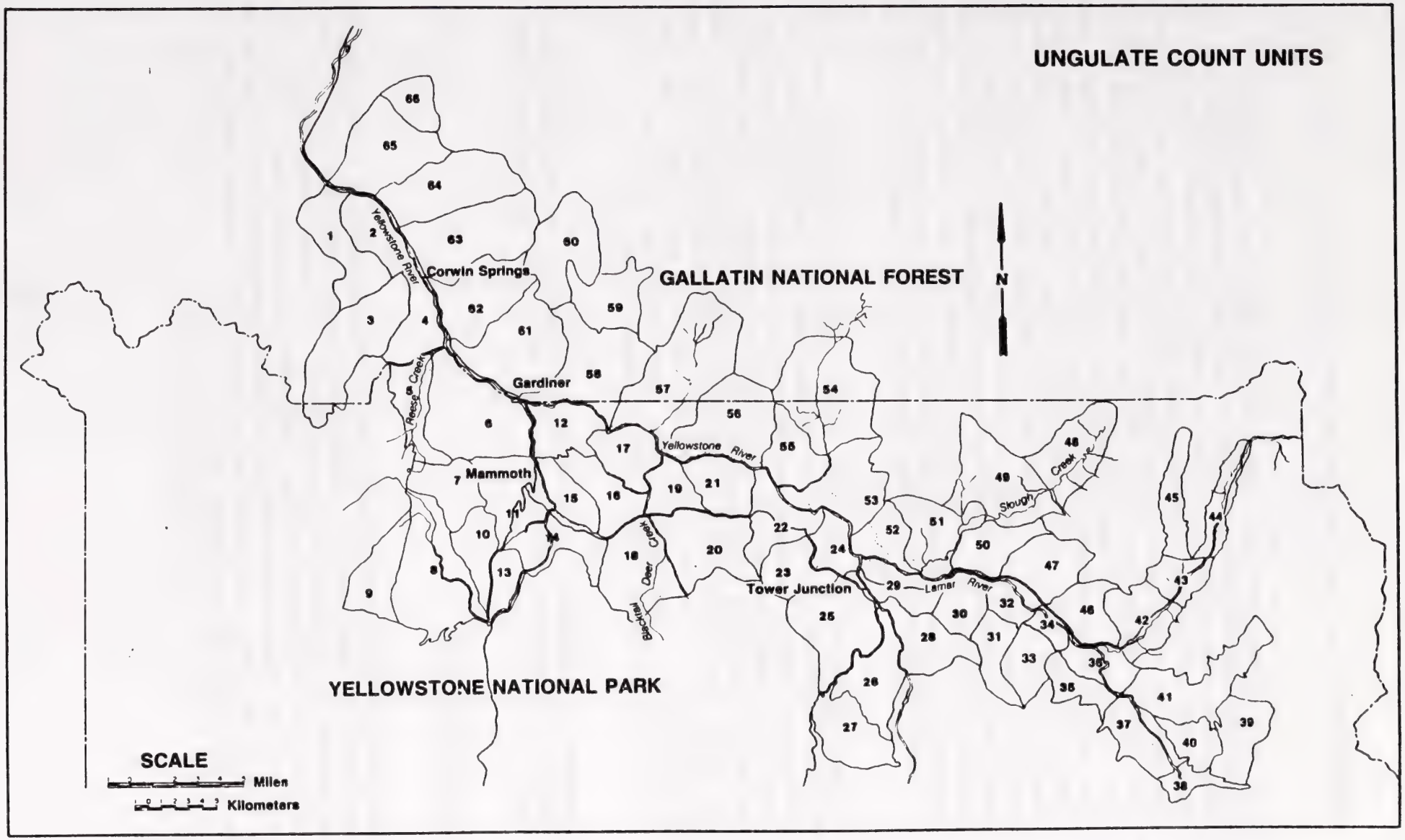

Fig. 1. Count units used in aerial surveys of elk, mule deer and moose on Yellowstone's northern elk winter range, 1985-89.

Mule Deer

Mule deer have increased from 1,007 in 1979 (Erickson 1979) to 2,217 (a 120% increase) in 1988 (Table 3). Surveys using helicopters proved 43%-62% more effective than Piper Super Cubs in seeing mule deer (Table 3). Time devoted to the count increased 75% between the 1979-1986 period and 1987-1988. The increase in search effort was largely a product of counting more mule deer and counting to higher snowlines. The winters of 1986-1987 and 1987-1988 were mild. Snowpacks averaged 70%-80% and 50%-70% of the average, respectively. The snowline was 480-800 m higher during the 1987 count than during the 1986 count, and the snowline was 300-800 m higher during the 1988 count than during the 1987 count. Aircraft typically flew only up to snowline since all of the deer were concentrated below snowline on green-up. As a result of higher snowlines, the size of the area counted increased in 1987 and 1988. Helicopter surveys of mule deer in the Bridger Mountains with similar terrain and vegetation yielded about a 66% sightability, (Mackie et al. 1980) suggesting the herd on the northern range might number at least 3,000 mule deer.

Highest densities of mule deer were in Count Units 2 and 4 west of the Yellowstone River and north of Yellowstone National Park (Figs. 1 and 2). These count units include most of the irrigated hay fields of the Royal Teton Ranch which provides additional mule deer habitat. Spring ratios of fawns per 100 adult mule deer have been very high in most years ($x = 45$, except for 1983 and 1989) corresponding to the dramatic increase in mule deer numbers since 1979 (Table 4). The mule deer count declined about 19% after the severe winter of 1988-1989. Fawn mortality was apparently high and late winter 1988-1989 fawn ratios were the lowest for the decade (Table 4).

Harvests of mule deer in the area have steadily increased during the 1980's; 1983 had the highest reported harvest on record for the area (Foss 1985, Table 4).

White-Tailed Deer

White-tailed deer were probably never common anywhere in Yellowstone National Park and they were rare on the northern range (Skinner 1929). The area lacks the extensive riverine deciduous shrubs and forests that typify white-tailed deer habitat in Montana (Allen 1968, Martinka 1968, Dusek 1981). Snow depths south of the Mammoth-Gardiner area appear excessive for white-tailed deer, although they have been observed to winter in thickets along the lower Gardner and Yellowstone Rivers along the park boundary. Yellowstone Park represents the very fringe of white-tailed deer habitat.

Table 3. Aerial counts of mule deer on Yellowstone's northern range, 1979-1989.

Year	Date of Count	Deer Counted	Pilot	Observer(s)	Aircraft
1979	---	572	D. Stradley	Houston	Super Cub
1979	4/3	1,007	M. Duffy	Erickson	Jet Ranger II
1986	3/4	706	B. Ferguson	Singer	Super Cub
1986	3/14-15	1,863	C. Rogers	Singer	Bell-206
1987	3/31-4/1	2,134	M. Duffy	Alt/Hoppe/ Singer	Jet Ranger II
1988	4/11-12	2,274	G. Ewen	Singer/ McClure	Helier 12-E
1989	4/30-5/2	1,796	R. Hawkins	Lemke/ Singer	Helier 12-E

Sources: Erickson (1979), Houston (1979), Singer (1986), Alt et al. (1987), Singer et al. (1988), Lemke and Singer (1989).

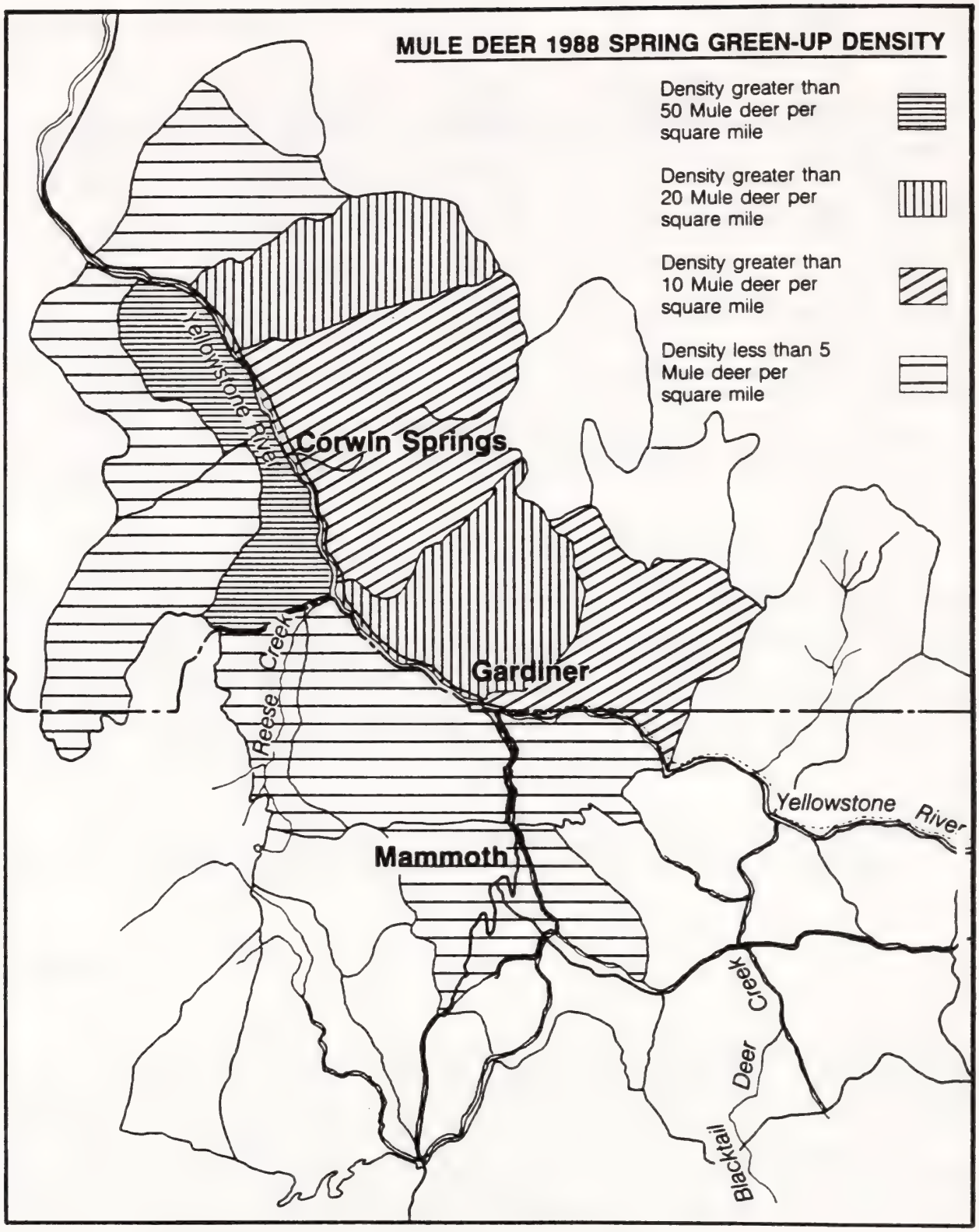

Fig. 2. Mule deer densities at spring green-up time on Yellowstone's northern range. (Count units correspond to those in Fig. 1).

Table 4. Deer harvest and classification data for Yellowstone's northern range north of the park boundary and east of the Yellowstone River (Hunting District 313).

	Posthunting Season (Dec.) Ratios				Spring Ratios				Harvests	
Year	Bucks: 100 Does	Fawns: 100 Does	Fawns: 100 Ads.	Sample Size	Fawns: 100 Ads.	Sample Size	Fawn Mortality(%)	Recruitment	Mule Deer	White-Tails
1979	17	67	52	345	32	1,108	23	29	234	9
1980	--	--	61	286	--	--	--	--	256	11
1981	15	65	56	97	40	300	29	29	504	27
1982	--	--	55	381	48	727	13	32	571	44
1983	7	65	60	303	29	420	52	23	746	11
1984	21	88	73	159	47	508	36	32	580	12
1985	0	42	42	68	44	562	0	31	404	33
1986	--	--	--	--	50	624	--	--	488	31
1987	--	--	--	--	47	2,134	--	--	358	17
1988	--	--	--	--	52	1,936	--	--	503	33
1989	4	41	38	745	14	1,796	--	--	--	--

Sources: Foss (1985), Alt et al. (1987), Singer et al. (1988), Lemke (1990).

Skinner (1927) reported that there were about 100 white-tailed deer on the northern range prior to 1916. Between 1914 and 1921 the population declined, and by 1924 white-tailed deer were gone altogether from the northern range (Skinner 1929). Supplemental feeding at Gardiner and Mammoth likely influenced white-tailed deer presence in the park during the early 1920's. Harvests suggest that white-tailed deer have increased substantially on the northern range just north of Yellowstone (Hunting Districts 313 and 314) during the 1980's (Table 4). Wildlife report cards from Yellowstone National Park files include 18 summer sightings of white-tailed deer within the boundaries of Yellowstone during the 1980's.

Moose

Moose reportedly colonized the area south of Yellowstone Lake and the Jackson Hole area by the 1870's (Houston 1982:158). Moose did not occur on the northern range or adjacent south-central Montana until around 1913 (Stevens 1971, Walcheck 1976, Houston 1982). These reports may represent an increase of moose, which were considered rare at the time, or moose that were returning after a period of absence.

Moose increased on the northern range and were abundant in Slough Creek by the 1930's and 1940's (McDowell and Moy 1942). The subsequent status of moose on the northern range is unclear. Chadde and Kay (1988), citing unpublished Gallatin National Forest files, reported that moose sightings by U.S. Forest Service personnel declined between 1940 and the early 1960's. Erickson (1979) reported moose numbers were relatively stable from 1961 to the late 1970's. Moose seen on elk distribution flights in 1969-1973 (Fig. 3) averaged 32 % 16 (x % S.D) in December and 45% 20 in May, but these counts declined to 17%9 in December and 27%10 in May for the years 1974-1977. Mean declines for December were 47% and for May 40% respectively ($t=3.68$, $df=4$, $p < 0.05$ for December; $t=1.67$, $df=7$, $p < 0.15$ for May). Counts in upper Slough Creek suggested a decline of moose in the mid 1970's with a recovery of population numbers by the late 1980's (Table 5). However, moose were seen twice as frequently during horseback moose surveys conducted in the 1940's compared to those of the 1980's (Table 6).

Houston (1982:169) conservatively estimated that there were 200 moose on the northern range in 1979. Moose harvests increased from 35 in 1979 to 47 in 1986 on areas bordering the northern range. If 200 moose existed on the northern range prior to the hunting season (Houston 1982:169), then these harvests corresponded to 18% and 24% of the population respectively. If moose did in fact increase in the 1980's (Table 4), then the harvest rates would be decreased. Montana hunting districts were realigned to better distribute the harvest and beginning in 1986, the number of permits was increased. The rationale for the increase was to decrease the population due to reduced carrying capacity and to increase the low calf ratios (Swenson 1985).

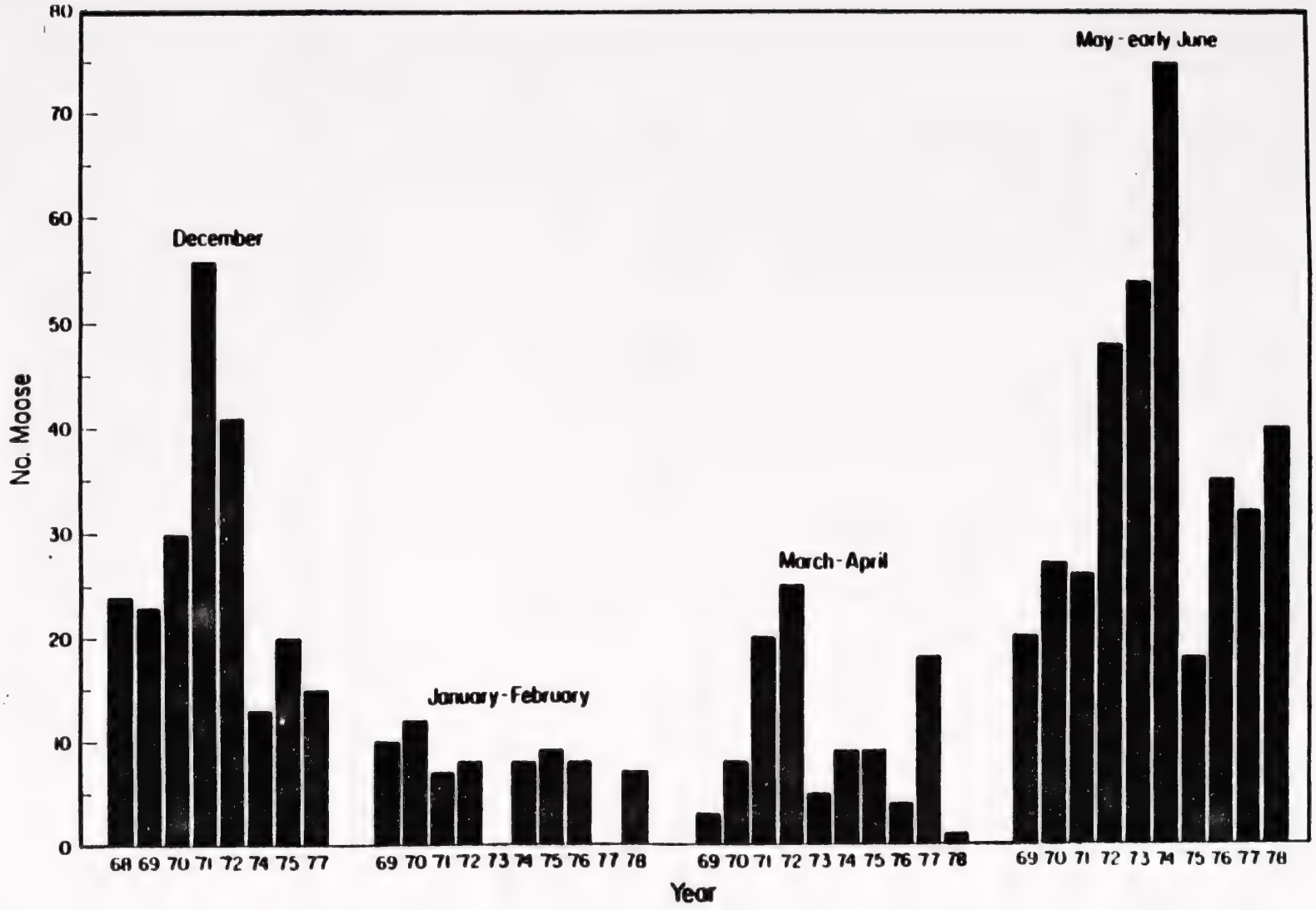

Fig. 3. Number of moose observed incidentally during elk distribution flights on Yellowstone's northern range from December to May of each year 1968-78 (Barmore 1980, Houston 1982). Upper Soda Butte and upper Hellroaring drainages were not surveyed.

Table 5. Highest counts of moose during 10 winters, 1968-1978, seen in specific locales incidental to elk counts on Yellowstone's northern range. Data from Barmore (1980) and Houston (1982).

	Below Mammoth	Gardner River-Mt. Everts	Above Mammoth-Gardner's Hole	Black-tail Plateau	Tower Area	Lower Slough Creek	Upper Slough Creek	Lamar Valley
1968-1969	4	3	4	1	4	1	14	6
1969-1970	5	2	11	2	5	3	10	3
1970-1971	2	1	5	7	9	10	13	5
1971-1972	3	1	16	8	14	25	27	6
1972-1973	1	3	6	0	13	14	14	1
1973-1974	3	3	4	3	14	14	23	11
1974-1975	3	3	7	1	4	7	6	2
1975-1976	5	4	6	2	13	15	3	2
1976-1977	1	1	3	3	12	6	9	3
1977-1978	1	3	4	2	8	2	11	7
1985-1986*	--	--	--	--	--	--	4	--
1986-1987*	--	--	--	--	--	--	14	--
1987-1988*	--	--	--	--	--	--	28	--
1988-1989*	--	--	--	--	--	--	29	--

*Locales other than Upper Slough Creek were not available for comparison 1985-1989.

Table 6. Summary of fall moose horseback counts in the northeast northern range (Upper Hellroaring, Buffalo Fork and Slough Creek drainages), Gallatin National Forest.

Year	Period	Party Days	Moose Seen	Moose Observed Per Day
1942	June-Oct.	100	194	1.94
1947	9/5-10/3	29	78	2.69
1948	9/4-9/29	26	53	2.04
1949	9/8-9/27	20	24	1.20
1985	9/11-9/20	23	12	0.52
1986	9/11-9/17	16	13	0.81
1987	9/9-9/14	22	20	0.90
1988	9/11-10/15	22	59	2.70
1989	9/11-9/17	34	36	1.06

Sources: Swenson (1985), Puchlerz (1986).

Northern Yellowstone Elk Herd

From 1970 to 1988 the northern elk herd was characterized by population growth, increased migrations north of the park, and increased hunter harvests as the herd recovered from the population reduction period.

The northern Yellowstone elk herd was reduced to less than 5,000 animals by 1968 due to artificial removals by park staff between 1935 and 1968. By the late 1970's counts increased to about 12,000 (Houston 1982). Population size averaged 9,026 between 1970 and 1974 (Houston 1982:17) and 11,906 from 1975 to 1980 (Table 7).

In the 1980's the northern elk herd steadily increased to a population of 18,913 in 1988. Population size averaged 16,488 from 1981 to 1988 (Table 7). Sightability of elk was about 86% during the winter of 1986-1987, and about 91% during the following winter (1987-1988). Bull ratios in the northern herd averaged 30 bulls:100 cows and calf ratios averaged 20 calves:100 cows from 1986 to 1988.

The percent of the northern elk herd migrating from the park averaged 7% between 1970 to 1974 (Houston 1982:29), 17% from 1975 to 1980, and 17% from 1981 to 1988. Elk became more available to hunters north of the park beginning in 1975. Harvest of the prehunt population averaged less than 1% from 1970-1974 (Houston 1982:17), 8% from 1975 to 1980 and 9% from 1981 to 1988 (Table 7). Bulls represented the majority of the late season harvest until 1981-1982 and the majority of the general season harvest until 1986-1987 (Table 7). Harvest prior to 1981, therefore, had proportionally less effect (if any) upon population growth.

Seven of the first eight winters in the 1980's received less than average precipitation. The 1988 drought caused a decline in forage production, the 1988 fires burned 39% of the northern winter range, hunters took an estimated 14%-16% of the herd, and another 24%-27% of the elk herd were winterkilled during the 1988-1989 winter (Table 7). The elk count declined to 10,908 in the late winter (Table 7). Elk sightability declined to to 60%. Deep crusted snow, smaller groups of elk and a greater tendency to use tree cover apparently reduced sightability of the winter count.

Bulls and calves died at a higher rate during the severe winter of 1988-1989. By late winter bull ratios were 18:100 cows and calf ratios were 7:100 cows (Singer et al. 1989). The typically low calf ratios for the northern elk herd (Houston 1982, Singer 1990), imply the potential for for a strong compensatory reproduction response by elk if wolves are restored to Yellowstone.

Table 7. Aerial counts, harvests, and sightability estimates of elk on Yellowstone's northern range, 1978-1989. These figures were extended to 1976-1977, the approximate year when elk began to recolonize the area north of Yellowstone Park following the 1960's reductions. Also, 1976-1977 marked the resumption of significant harvests north of the park and an increase in the elk herd's carrying capacity as a consequence of the resumed migration.

Year	Actual Early Winter Count	Actual Count In Park	Actual Count North of Park	Estimated Prehunt Population Count Size[1]	Sightability Corrected Prehunt Population[2]	Total Harvest[3]	% of Prehunt Count (or of Corrected Count) Harvested	% Bulls in Harvest General	% Bulls in Harvest Late	% Total Harvest in Late Hunt
1974-1975	12,518	4,537	2,697[7]	12,545	--	147	1	48	no hunt	0
1975-1976	11,665[4]	8,812	2,853[7]	12,405	--	1,401	11	74	68	86
1976-1977	12,813[4]	10,409	1,945[7]	12,901	--	88	1	82	no hunt	0
1977-1978	12,680	5,981	3,039[7]	13,483	--	952	7	81	56	84
1978-1979	10,318	10,549	2,392	10,516	--	268	3	78	86	26
1979-1980	11,108	9,566	637	10,226	--	605	6	79	61	80
1980-1981[5]	--	--	--	--	--	247	--	84	56	54
1981-1982	16,019	14,922	1,097	16,462	--	1,234	7	90	48	82
1982-1983[5]	--	--	--	--	--	1,804	--	95	33	81
1983-1984[5]	--	--	--	--	--	1,955	--	78	24	85
1984-1985[5]	--	--	--	--	--	1,419	--	75	14	75
1985-1986	16,286	13,288	2,998	16,599	--	1,371	8	80	12	77
1986-1987	17,007	15,284	1,723	17,773	--	1,595	9	52	8	52
1987-1988	18,913	18,430	483	19,000	21,075-22,961	215	1 (0.9)	--	5	77
1988-1989	10,908[6]	5,618	5,290	12,608	17,207-19,059	2,773	22 (15)	--	2	--

[1] Most early winter counts were conducted Dec. to Jan. following the general hunt (approximately 19 Oct. to 30 Nov.) and either preceded the late hunt (usually 15 Dec. to 15 Feb.) or during the early part of the late hunt. The total elk taken during hunts on the date of the count were added back into the actual early winter count to estimate the prehunt size. The prehunt population size for 1975-1976 was reconstructed from a more successful spring green-up count on May 7-8, 1976.

[2] The sightability correction is further described in Singer et al. (1989).

[3] Both the general (Oct. to Nov.) and special late (Dec. to Feb.) hunts were combined.

[4] Houston (1982:16,23) subtracted elk harvested by the date of the aerial count, 1976-1980, in order to report a late winter population size. To be consistent, we added those removals back in.

[5] No counts were made these winters.

[6] The 1988-1989 early winter count was a poor count and was conducted after elk had dispersed into forests.

[7] Maximum counts of elk outside Yellowstone Park occurred later during the winter than the early winter counts on Apr. 12-13, 1975; Dec. 17-18, 1976; Jan. 30, 1978.

Elk in the Remainder of Yellowstone National Park

In 1987-1988, an estimated 31,000 elk summered, and approximately 22,000 elk wintered within the park boundaries (Table 8). Significant portions of seven different elk herds and a few animals from an eighth herd, the Carter Mountain herd, summer within Yellowstone National Park (Fig. 4). Radiocollared elk were representative of all sex groups, age groups, and capture sites on winter ranges; thus, these figures are probably useful as tenuous but preliminary estimates.

Elk from more than one herd share several summer ranges in Yellowstone National Park. Two summer ranges are shared by three herds: 1) the Madison Plateau (occupied by the Madison-Firehole, Sand Creek, and northern herds); and 2) the Madison-Firehole area (occupied by the Madison-Firehole, Gallatin, and northern herds). In the Upper Yellowstone River-Thorofare area (Fig. 4), as many as four elk herds (Jackson, North Fork Shoshone, northern, and possibly a few elk from the Carter Mountain herd) share a common summer range. Summer ranges in the central and north-central portions of the park are only occupied by the northern herd.

A few changes in elk summer distributions occurred. About 800 elk from the Jackson herd once migrated northeast of Jackson Lake to summer on the Pitchstone Plateau (J. Yorgason pers. comm., B. Smith, unpubl. data). This segment may have been eliminated due to extensive hunting on Uhl Hill of elk which which had traveled across Burned Ridge and Antelope Flats towards the National Elk Refuge. Alternatively, there may have been a natural shift in migration patterns (M. Boyce pers. comm.). In either case, the Pitchstone Plateau is now occupied in summer primarily by the Sand Creek herd (Brown 1985).

Portions of four elk herds totaling about 22,000 (prefire), wintered within the Yellowstone National Park boundaries (Table 8). About 85% of the northern herd, more than 98% of the Madison-Firehole herd, 31% of the Gallatin herd and about 500 additional elk (mostly from the North Fork Shoshone herd) wintered within the park.

A small number of elk wintered in scattered thermal areas. A survey on 16 April 1988 counted 31 elk in small thermal areas including 11 elk in the Bechler Meadows area, 11 elk in the Heart Lake Geyser Basin, five elk at Hot Springs Geyser Basin, and four elk near West Thumb Geyser Basin.

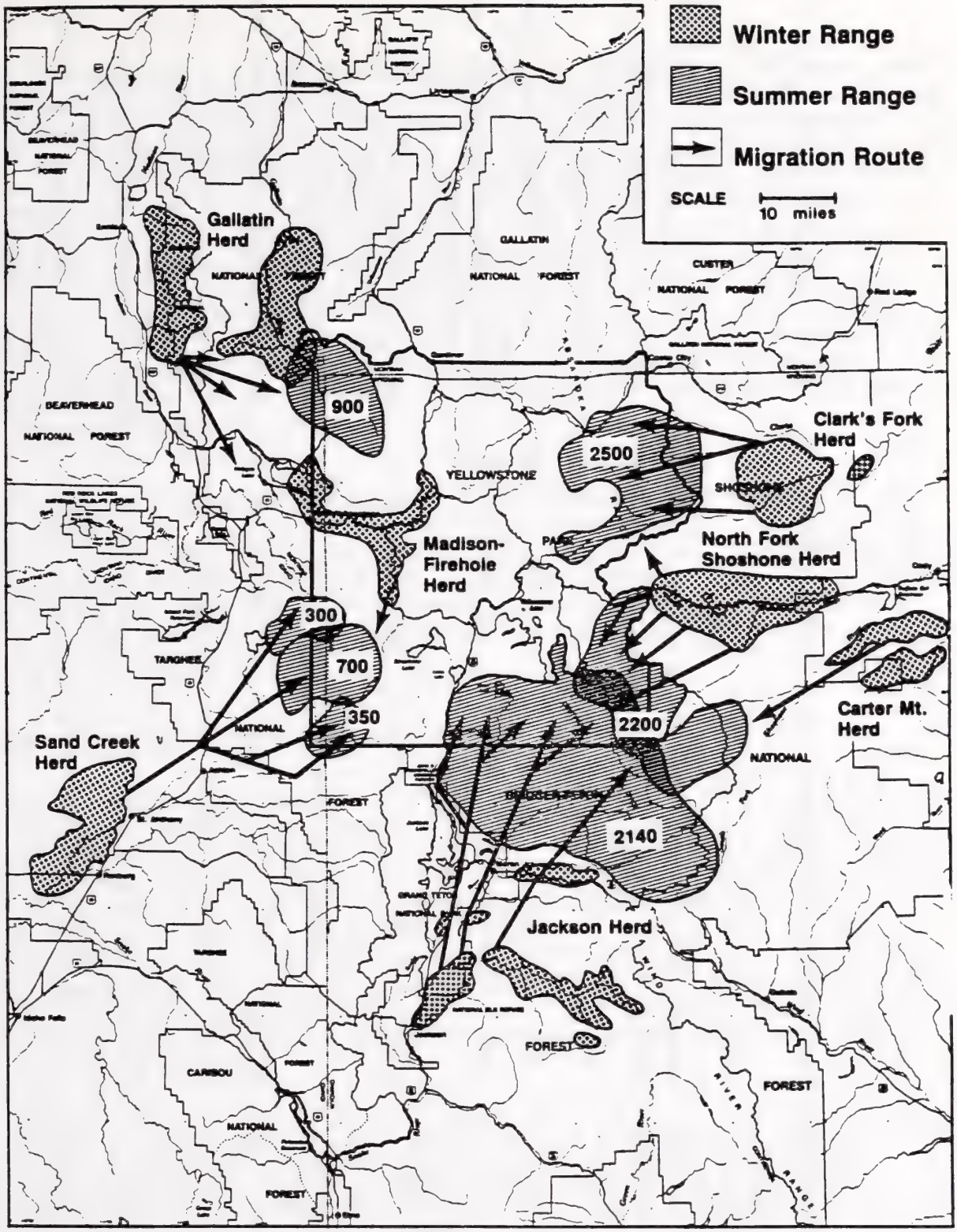

Fig. 4. Map showing the approximate winter ranges and summering areas for 7 elk herds other than the northern herd that use Yellowstone National Park.

Table 8. Estimates of elk summering in Yellowstone National Park for the period, 1984-1988.

Name of Herd	Herd Size	Proportion of Radio-collared Elk Summering in Yellowstone	Sample Size of Collared Elk	Est. No. Elk Summering in Yellowstone	Mean No. Wintering in Yellowstone	Years of Radiolocation Data	Days Spent on Summer Range	Summer Locations
Gallatin	1,850[c1]	.48	72	900	580[c]	1969-1986	150	Gallatin Range, Specimen Creek
Sand Creek	4,900[e]	.21	84	1,056[e]	0	1981-1987	138	Bechler Meadows, Madison Plateau, Chick Creek
Jackson	11,000[e2]	.28	85	3,080	0	1978-1982	150	Thorofare, Two Ocean Plateau, Big Game and Chicken Ridges
Carter Mountain	2,550[e]	tr	0[3]	100+	0	1986-1988	--	South Fork Shoshone
N. Fork Shoshone	2,600[e]	.78	18	2,020	0-500	1979-1980	160	Signal Hills, Thorofare
Clarks Fork	3,180[e]	.83	18	2,600	0	1979-1980	160	Upper Lamar, Pelican Valley, Mist Creek
Northern	21,000[e]	.98	68	20,580	17,457	1985-1988	140	All of Yellowstone Park
Madison-Firehole	800[c]	1.00	6	800	800	1965-1966	--	Madison drainage, Madison Plateau
Total				31,136	20,380-20,880			

c = count

e = estimate

[1] Vales and Peek (1990) concluded this number is an underestimation of the herd size.

[2] A 1989 model revises the estimate for the Jackson herd to over 16,000 elk for 1987 and 1988 (Lockman et al. 1989).

[3] No radiotelemetry studies were conducted on the Carter Mountain herd. Such a study is scheduled for 1990 (L. Roop pers. comm.).

Sources: Cada (1970-1975), Craighead et al. (1973), Taylor (1978-1986), Rudd (1982), Brown (1985), Davidson et al. (1985, 1986), Yorgason et al., (1986), Boyce (1989), Vore (1990), B. Smith (in prep.), D. Vales (unpubl.).

Population trends have varied considerably among the herds. The Sand Creek herd increased fivefold from 1959 to 1983, but has been relatively stable or slowly increasing from 1983 to 1988 (Chu et al. 1988). Present management goals in the Sands Management Plan call for no further growth of the Sand Creek herd due to potential conflicts with livestock grazing (Trent et al. 1985), and aim to keep the herd to a count of 2,000 posthunt on the winter range (J. Naderman Idaho Game and Fish, pers. comm.). The Madison portion of the Gallatin herd, however, grew to about 650 elk in the 1980's (Taylor 1984). Counts of the Madison-Firehole elk herd declined 21% during the 1980's (F. Singer and G. Bowser, Natl. Park Serv., unpubl. data). Six aerial counts conducted from 1965 to 1980 averaged 763 elk (range 593-959), whereas eight counts conducted 1985-1988 averaged only 601 elk (range 487-736). No sightability correction is available for these counts, and therefore, the trends are speculative.

Harvest levels on the eight elk herds varied considerably (Table 9). The Jackson, Sand Creek, and Gallatin herds were harvested near, at, or above maximum sustained yield (Table 9, Boyce 1989). Boyce (1989) calculated that the Jackson herd harvest averaged 86% of maximum sustained yield. Harvests of the North Fork Shoshone and Clarks Fork herds were more moderate, while harvests of the northern and Madison-Firehole herds averaged 9% and less than 1% respectively (Table 9).

Potential Prey Base for Wolves

From 1980 to 1988, an average of 14,491 ungulates on the northern range and 4,130 ungulates on other park ranges were completely available to large predators (Table 10). Ungulates occurring in the Yellowstone River canyon between Gardiner and Dome Mountain, Montana, (average 4,064 ungulates) were judged to be less available to wolves because of 800 year-round human residents and extensive road access. From 1980 to 1988, there were about 22,685 ungulates in Yellowstone Park during the winter. The total summer in-park ungulate population may have exceeded 37,804 (Table 10). When considering only ungulates completely available to wolves and a minimally-recovered population of 100 wolves, initial wolf to ungulate ratios parkwide would be 1:225 in winter and 1:378 in summer.

Keith (1983) reported wolf to ungulate ratios of 1:96-328 for wolf-occupied areas of North America. A minimally-recovered population of wolves in Yellowstone would be on the high side of these ratios. Theberge (in review) cautioned that wolf:prey ratios be used for preliminary assessments only. He argued that functional responses in wolf predation, lags in numerical responses of wolves, variable rates of prey switching, variable use of nonungulate prey, and the proximity of ungulates to their nutrient-climate ceiling greatly complicated use of wolf:prey ratios. Wolf predation tends to be compensatory with starvation when the ungulate population is near ecological carrying capacity and thus of less population consequence, but wolf predation is additive to other mortality below that level (Theberge and Gauthier 1985).

Table 9. Estimated population sizes and harvests of eight elk herds inhabiting Yellowstone National Park, 1980-1987.

Elk Herd	Population Size	Mean Harvest	Period	Sex and Age Classes Harvested: Spikes	Mature Bulls	Mature Cow	Calves	Source
Jackson	11,000[e]	2,913	1950-1987	--	818	--	1,048	320	Boyce (1989)
Sand Cr.	4,900[e]	966	1981-1987	310	297	359[1]			Trent et al. (1987)
Gallatin[2]	2,500[c]	912	1980-1985	320	342	219	31		Taylor (1981-1986)
N. Fork Shoshone	2,600[e]	570	1982-1987	122	245	180	23		Yorgason (1987)
Clarks Fork	3,180[e]	713	1982-1987	103	236	313	61		Yorgason (1987)
Carter Mountain	2,550[e]	658	1982-1986	162	170	262	64		Yorgason (1987)
Madison-Firehole	800[c]	<20	1980-1988	--	--	--	--		Craighead et al.
Northern	18,986[se]	1,401	a) 1980-1986, reg.	87	132	73	106		
			b) 1980-1987, late	59	198	574	207		Foss (1987)

c = count
e = estimate
se = sightability estimate

[1] The antlerless category includes calves, but the numbers were not available.

[2] In this case, elk numbers and harvests on the southeast side of the Madison Valley are incl ded (e.g., Hunting Dist. 360).

Several harvest rates are likely overestimated, since population sizes are likely underestimated.

Table 10. Minimum numbers of ungulates available to large predators in Yellowstone National Park prior to and immediately after the drought, fires, and the severe winter of 1988-1989. Those ungulates that typically winter near Gardiner, Montana, and are less available to wolves are listed separately.

	Winter Counts[1]						
	Northern Winter Range						
	Mean 1980-1988						Summer Estimates
Species	Completely Available to Wolves	Less Available to Wolves Near Gardiner	Total Northern Range, Low and High Counts 1980-1988	All of Northern Range Postfire, 1989-1990	Other Winter Ranges[2] 1988	1989	(All Yellowstone Park, Including Northern Range) 1980-1988
Elk	15,681	1,776	10,226-19,000	15,000	1,900	600	31,136
Bison	433[3]	0	233-594	457	~2,000	<2,000	>2,500
Pronghorn	100	292	102-495	372	0	0	495
Mule Deer[4]	~100	1,714	1,007-2,274	1,796	<30	<30	>3,000-
Bighorn Sheep[5]	~176	160-180	300-600	--	--	--	>273
Moose	200[e]	a few	--	--	>100	>50	>300[6]
White-tailed Deer	<10	<100	--	<100	0	0	<100
Total	14,491+	4,064+	--	15,418+	4,530+	2,680	37,804+[6]
Ungulates:wolf for 100 wolves	:145	:41	--	:154	--	--	:378

e = estimate from Houston (1982).

[1] Actual counts for all species. Average counts are provided for the period 1980-1988 except for pronghorn and bighorn where only recent counts are provided since pronghorn were still recovering from reductions and bighorn from a disease outbreak (Meagher in prep.). Elk and bison counts were conducted during early winter; mule deer and pronghorn counts were conducted during spring green-up (Mar.-Apr.).

[2] Includes Madison-Firehole, Pelican Valley, Upper Yellowstone River-Thorofare.

[3] Mean of counts, 1980-1987 (Meagher 1989).

[4] Mule deer numbers parkwide are almost totally unknown, however, most of the mule deer from the northern range are suspected to migrate each summer into the park. Summer mule deer numbers for the entire park are likely several times that of the northern herd.

[5] Data from Meagher (pers. comm.) for 1980-1988. Winter ranges north of the park included both Cinnabar Mountain and Spring Creek areas. Also, an unknown number of bighorn sheep occupy the Thorofare Creek-Trident area of the park.

[6] Moose and mule deer parkwide in summer are likely greatly underestimated.

Recovery of elk populations will take several years. The events of 1988, including the reduction of forage due to drought and the burning of winter ranges in the fall followed by a severe winter resulted in an increase in harvests and winterkill of ungulates (Singer et al. 1989). Reductions in most ungulate populations were between 10% and 20%. However, the northern Yellowstone elk herd declined about 40%, and the Madison-Firehole elk herd probably declined more than 50% (Singer et al. 1989). Elk calf crops were reduced in 1989 apparently as a consequence of the severe winter (Singer et al. 1989).

Research over the next few years is directed at documenting the effects of the 1988 fires upon elk populations and habitat relationships. The carrying capacity of Yellowstone's elk ranges are predicted to increase as a result of the 1988 fires. Herbaceous and shrub production (Lyon and Stickney 1976) along with protein content and palatability will likely increase in forages returning on burned areas (Spalinger et al. 1986). Winter range enhancement may be very brief; the positive effects of burning on grasses and forbs often lasts only 1-2 years (Hobbs and Spowart 1984, Wood 1988). Summer range enhancement may be more significant than winter range effects. Many new forest openings will be created, and herbaceous and shrub vegetation will increase in burned forests; however, elk summer range may not have limited population size before the fires. In either case, the recovery of the park's ungulates, including elk, to at least prefire levels would likely have to occur before wolves could feasibly be reintroduced and recovered in the park.

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THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK; II

John A. Mack, Francis J. Singer, and Mary E. Messaros
U. S. Department of the Interior
National Park Service
P. O. Box 168
Yellowstone National Park, Wyoming 82190

THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK II: Elk, Mule Deer, White-tailed Deer, Moose, Bighorn Sheep, and Mountain Goats in the Areas Adjacent to the Park.

John A. Mack, Francis J. Singer, and Mary E. Messaros
National Park Service, Division of Research,
Yellowstone National Park, WY 82190

EXECUTIVE SUMMARY

Elk

Portions of eight elk (Cervus elaphus) herds occupy Yellowstone National Park during the summer with 25,000-31,000 elk summering in the park annually in the 1980s. Summer estimates of the eight herds total 36,000-49,000 elk; including animals that summer outside the park. Winter ranges for three herds (Carter Mountain, Jackson, and Sand Creek) are quite distant from areas gray wolves (Canis lupus) would likely occupy. Portions of four elk herds, totaling about 13,480-20,880 elk, winter within Yellowstone National Park. These four herds include portions of the northern herd (11,600-19,000 elk), the Gallatin herd (about 580), the Madison-Firehole (800-1,400), and the North Fork Shoshone herd (Thorofare group, about 500 elk). Annual harvests for the eight herds averaged 7,032 elk during the 1980s.

Population Trends

During the last 20 years, population estimates for eight elk herds increased dramatically by about 17,000 elk (80% increase). Population estimates for the Sand Creek and northern range herds increased about fourfold. The Jackson and Madison-Firehole herds remained relatively stable. The Gallatin herd was reduced but then increased slightly during the last 20 years. Population estimates of elk from seven herds increased an average of 38% (range 10%-67%) during the 1980s (Table 1). Only the Madison-Firehole herd declined. Currently, elk numbers for the Jackson, Carter Mountain, North Fork Shoshone, Clarks Fork, and Sand Creek herds exceed management goals.

Migrations

Seven elk herds are strongly migratory and the Madison-Firehole herd is nonmigratory. Distances between winter and summer ranges vary from 8 km to 64 km (5-40 miles). Spring migrations to summer range for the Sand Creek herd lasted 46 days. Calving for migratory elk typically occurs enroute to summer ranges; except during springs with less snow when calving may occur on summer ranges. Calves born to elk migrating long distances may occasionally be

Table 1. Elk population statistics for 8 elk herds located within and/or adjacent to Yellowstone National Park (YNP) during the 1980's.

Herd Unit	Estimated Population Size	Mean Harvest 1980's	Percent Population Change 1980's	Percent Herd That Summer in YNP[1]	Mean Days in YNP During Summer	Distance (km) of Winter Range From YNP	Sex and Age Class of Harvest (%)			
							Spike Bulls	Bulls	Adult Cows	Calves
Gallatin	2,500	912	+20[2]	48	150	includes YNP	35	37	24	3
Northern	16,500-21,000	1,401	+31	90	---	includes YNP	10	23	45	22
Clarks Fork	3,000	713	+67	83	160	32	14	33	44	9
North Fork Shoshone	2,800	570	+64	78	160	8-13	21	43	32	4
Carter Mountain	3,000	658	+55	a few	---	48	25	26	39	10
Jackson	11,000	2,530	+18	28	150	48	|--53[3]--|		36	11
Sand Creek	3,800-4,900	914	+10	21	138-150	64	32	31	37[4]	---
Madison-Firehole	800-1,400	tr	decline	100	---	includes YNP	---	---	---	---
Total	43,400-49,600	7,698								
Mean			+38							

[1] Based upon movements of 386 radio collared elk.
[2] Increase occurred almost entirely in the Madison River segment of the herd.
[3] Includes spikes and bulls.
[4] Includes some calves.

Sources: Craighead et al. (1973), Houston (1982), Rudd (1982), Rudd et al. (1983), Brown (1985), Trent et al. (1985), Carlson (1987), Yorgason et al. (1987), Hurley et al. (1989), Boyce (1989), Singer (1990), B. Smith per. commun.

available to wolves. Use of summer ranges in Yellowstone varied from 138 to 160 days (Table 1). Fall migrations to winter ranges averaged 19 days for the Jackson elk herd and 27 days for the Sand Creek herd. Migration patterns changed little over the past 20 years. Exceptions include: a) a higher proportion of northern range elk summer west of Yellowstone Lake, b) a former migration of about 800 elk from the Jackson herd to southwest Yellowstone National Park (Cole 1969) was reduced to 100-150 by the late 1970s (B. Smith, in prep.), c) the proportion of Jackson elk migrating into Yellowstone National Park and the Teton Wilderness through the Togwotee Pass area has declined.

Mule Deer

North and Northwest of Yellowstone National Park

Mule deer (Odocoileus hemionus) populations increased dramatically north of Yellowstone National Park in Montana. Helicopter counts of mule deer on the northern range increased 78% (from 1,007 to 1,795) during the 1980s (Table 2). An increase in the harvest in the upper Gallatin suggests mule deer may have increased there also. Deer harvests averaged 726 per year, of which about 9% were white-tailed deer (Odocoileus virginianus). Antlerless harvests in Montana increased fivefold during the 1980s due to management efforts to reduce deer populations. A few mule deer from other areas in Montana may migrate into Yellowstone National Park. Two adult does marked on the Boulder River summered near Slough Creek campground and one doe from the Bridger Mountains summered near Madison Junction.

East of Yellowstone National Park

Mule deer population estimates east of the park increased about 77% during the 1980s to about 14,000 according to computer models (Table 2). Harvests averaged 1,599 per year during the 1980s. Some mule deer from the Clarks Fork, North Fork Shoshone, and South Fork Shoshone probably migrate into Yellowstone National Park for the summer.

South of Yellowstone National Park

About 2,000-2,600 mule deer occur in the Jackson and Targhee herd units south of Yellowstone National Park (Table 2). Population estimates have doubled during the 1980s but some of the increase may have been due to new methods of estimating herd size. Harvests averaged 685 per year during the 1980s.

West of Yellowstone National Park

Mule deer numbers for the Sand Creek herd averaged 1,599 for five trend counts during the 1980s. Few deer from the Sand Creek herd summer in Yellowstone National Park. The herd appears to be increasing.

Table 2. Mule deer population statistics in areas adjacent to Yellowstone National Park (YNP) during the 1980's.

Herd Unit	Estimated Population Size	Mean Harvest 1980's	Percent Population Change 1980's	Extent of Summer Migration Into YNP	Distance (km) of Winter Range From YNP	Sex and Age Class of Harvest (%)		
						Adult Males	Adult Does	Fawns
North of YNP[a]								
Upper Gallatin	---	130	increasing	extensive	borders YNP	---	---	---
Northern Range	3,000	596+[b]	+78	extensive	borders YNP	---	---	---
East of YNP								
South Fork Shoshone	4,800	792	+16	probable	27	78	21	1
North Fork Shoshone	2,500	242	+108	probable	48	85	15	tr
Clarks Fork	7,000	565	+123	probable	32	80	19	1
South of YNP								
Jackson	1,200-1,600	608	+250	probable	48	66	32	2
Targhee	800-1,000	77	+82	probable	24	83	17	0
West of YNP								
Sand Creek	1,337-1,983	256	counts sporadic	limited	16-48	70	30[c]	---
Total	20,637-21,883	3,266						
Mean			+110					

[a] An unknown number of deer from the Boulder and Stillwater Rivers may migrate into YNP as evidenced by several marked individuals (Claire Simmons, Mont. Dept. Fish Wildl. and Parks, Big Timber, pers. corres.).

[b] Does not include the harvest in a small portion of Hunting District 314 which lies on the northern winter range.

[c] Includes some fawns.

Sources: Foss (1987), Kuck et al. (1989), Hurley et al. (1989), Lockman et al. (1989).

White-tailed Deer

Occasionally white-tailed deer are seen in Yellowstone National Park during the summer, however, no winter sightings occur within the park. Healthy or expanding white-tailed deer populations winter distant from areas wolves would likely occupy. Examples in Montana include Tom Miner Creek, Rock Creek, Yellowstone River downstream from Point of Rocks, Stillwater River, and the Boulder River. Examples in Idaho include Conant Creek and the Snake River. Therefore, wolf restoration is not predicted to affect white-tailed deer.

Moose

North and Northwest of Yellowstone National Park

Moose (Alces alces) on the northern range in Montana increased during the early 1980s with indices suggesting the population was relatively stable during the late 1980s (Swenson 1985a, Singer 1990). The moose population was estimated at 200 animals ten years ago (Houston 1982). A sightability-corrected estimate of population size is in progress. Average harvest north and northwest of the park was 116 moose (Table 3).

East of Yellowstone National Park

Moose populations east of the park are believed to be relatively stable except for the Thorofare area where they may have declined. An average of 44 moose were harvested annually (Table 3). The Thorofare area (bordering the southeast corner of the park) accounted for 55% of the moose harvest east of the park but permit numbers for this area were reduced during the 1980s. The Thorofare herd unit includes the best moose habitat. The North and South Forks of the Shoshone River include marginal habitat. In the Sunlight Basin herd unit losses of riparian habitat have occurred on private land.

South of Yellowstone National Park

An estimated 2,600 moose occupy the Jackson and Targhee herd units south of the park. Trend counts for the Jackson herd increased 78% during the 1980s. Some of this increase may be due to the greater efficiency of the counts. Population models suggest the Jackson and Targhee herds increased 5% and 130%, respectively, during the 1980s. Average harvest was 360 moose per year (Table 3). Moose migrate from Jackson and Targhee herd units into Yellowstone. Moose migrations from the Jackson herd into Yellowstone National Park were verified by radiotelemetry. Biologists estimate 40% of the Targhee herd summers in Yellowstone National Park.

West of Yellowstone National Park

Counts of moose west of the park in Idaho averaged 435 in the early 1980s. No counts were made between 1982 and 1987. In December 1988, during a fixed wing survey 923 moose were observed. Harvests averaged 25 and other known losses (illegal kills, road kills, etc.) averaged seven per year (Table 3). Moose occupy four winter ranges 8 km-56 km (5-35 miles) from Yellowstone National Park. Marking studies suggested about 1/4 of the moose from the Falls River herd (nearest the park) spent the summer in Yellowstone National Park. A few animals from the other herds may also migrate into the park.

Bighorn Sheep

North and Northwest of Yellowstone National Park

During the last 20 years, bighorn sheep (Ovis canadensis) populations increased in Montana north of the park. The Mount Everts-Specimen Ridge herd increased fourfold from 1965 to 1979. Bighorns recolonized the Cinnabar Mountain herd in 1965 and between 1967 and 1977 increased from 16 to 120 animals. All northern populations remained stable or declined slightly during the 1980s except the Mount Everts-Specimen Ridge population which had a major dieoff in 1982 due to a infectious keratoconjunctivitis epidemic. A minimum of 406 bighorn sheep are found north of the park (Table 4). Harvests declined during the 1980s and averaged 22 legal rams. Most bighorns from the Tom Miner, Cinnabar Mountain, and Mount Everts-Specimen Ridge populations migrate into Yellowstone National Park.

East of Yellowstone National Park

Bighorn sheep from the Clarks Fork, Trout Peak, Wapiti Ridge, and Younts Pea: herds east of the park increased an average of 7% during the 1980s (Table 4) These four herds total about 2,900 bighorns. Annual harvests averaged 91 legal rams. All four herds range near Yellowstone National Park but only limited migrations occur into the park. Wapiti Ridge is the exception with year-round ranges found in the Thorofare-Trident area of the park.

South of Yellowstone National Park

Bighorn sheep from the Targhee and Jackson herds range south of Yellowstone National Park. Occasional bighorn sightings on Mount Sheridan (in the park) may include individuals from the Targhee herd. The Jackson herd probably ranges outside areas wolves would likely inhabit. The Targhee and Jackson herds consist of about 100 and 500 bighorns, respectively. Populations of both herds were relatively stable during the 1980s. Annual harvests averaged 17 legal rams during the 1980s (Table 4).

Table 3. Moose population statistics in areas adjacent to Yellowstone National Park (YNP) in the 1980's.

Herd Unit	Estimated Population Size	Mean Harvest 1980's	Percent Population Change 1980's	Extent Summer Migration Into YNP	Distance (km) of Winter Range From YNP	Sex of Harvest (%) Adult Males	Adult Females	Calves
North of YNP								
Northern Range[a]	200	36	stable	includes YNP	includes YNP			
Upper Gallatin[b]	---	17	---	extensive	8-16	---75	17	8
Hebgen Lake[c]	---	63	---	extensive	includes YNP			
East of YNP								
Crandall	---	9	---	possible	---	100	---	---
Sunlight Basin	---	5	---	probable	3	100	---	---
North Fork Shoshone	---	3	---	probable	48	100	---	---
South Fork Shoshone	---	3	---	possible	48	100	---	---
Thorofare	---	24	---	includes YNP	includes YNP	100	---	---
South of YNP								
Jackson	2,300	329	greatly increased	verified[e]	---	76	21	3
Targhee	300	31	+130	probable	---	86	11	3
West of YNP								
Fall River	149[d]		stable	verified[f]	8	100	---	---
Big Bend	-----220	---------25	stable	probable	32	100	---	---
Junipers			stable	few/none	56	100	---	---
Island Park	192		stable	few/none	19	100	---	---
Total		545						

[a] Includes Montana hunt districts 316, 317, 318, 322, 328.
[b] Includes Montana hunt districts 306, 314.
[c] Includes Montana hunt districts 307, 309, 310, 361.
[d] Actual aerial counts.
[e] One radiocollared cow captured in the Buffalo Fork summered in YNP (Garvis Roby, Wyom. Dept. Game and Fish, Jackson, pers. corres.).
[f] 24% of marked moose migrated into YNP (Ritchie 1978).

Sources: Ritchie (1978), Houston (1982), Trent et al. (1984), Alt and Foss (1987), Chu et al. (1988a), Hurley et al. (1989), Lockman et al. 1989.

Table 4. Bighorn population statistics in areas adjacent to Yellowstone National Park (YNP) during the 1980's.

Herd	Estimated Population Size	Mean Harvest[a] 1980's	Percent Population Change 1980's	Extent Summer Migration Into YNP	Distance (km) of Winter Range From YNP
North of YNP					
Spanish Peaks (301)[b]	---	4	---	none	32
Taylor-Hilgard (302)	---	3	---	none	16
Cinnabar Mountain (300)	80-130	----8	stable	most herd	13
Tom Miner (300)	80-100		declined	most herd	5-8
Mount Everts-Specimen Rdg. (303)	136[c]	2	declined[d]	most herd	includes YNP
Stillwater (500)	40-50	3	declined	none	48
Rosebud (501)	70-100	2	stable	possible	32
East of YNP					
Clarks Fork	500	13	stable	a few	5-8
Trout Peak	500	19	+14	a few	13
Wapiti Ridge	1,000	28	+14	includes YNP	includes YNP
Younts Peak	900	31	stable	a few	13-24
South of YNP					
Jackson	500	15	stable or slight decline	none	56
Targhee	100	2	stable	a few	24
West of YNP					
No nearby populations					
Totals	3,906-4,016+	130			

[a] Harvest consists of 3/4-or-larger curl rams.
[b] Montana hunting district numbers in parenthesis.
[c] Actual count of sheep from Mount Everts along the Yellowstone River to the Specimen Ridge area.
[d] Population reduced by a pinkeye epidemic in 1982 (Meagher 1982).

Sources: Houston (1982), Keating (1982, 1985a), Meagher (1982), Hurley (1985), Irby et al. (1986), Hurley et al. (1989), Lockman et al. (1989), M. Meagher pers. commun.

Mountain Goats

Less than 100 mountain goats (Oreamnos americanus) inhabit areas adjacent to Yellowstone where wolves might occur (Table 5). About 8-12 mountain goats actually occur within the park. Some potential for mountain goat increase exists and Laundre' (1990) predicted Yellowstone National Park could possibly support 100-500 individuals.

Table 5. Nonnative mountain goat populations in areas adjacent to Yellowstone National Park (YNP)(adapted from Laundre' 1990).

Herd Unit	Estimated Population Size	Distance (km) from Yellowstone National Park
North of YNP		
Absaroka	100	0-24
Gallatin Range	a few	0-45
East of YNP		
Beartooths	150-180	19
South of YNP		
Palisades	250	80
West of YNP		
Spanish Peaks-Hebgen Lake	300	10-24
Total	800-830	

Information Needs

If wolves are reintroduced into Yellowstone National Park, more information will be required for ungulate herds subjected to both wolf predation and hunter harvest. The following state-of-the-art information should be obtained for each herd unit:

1. Annual aerial trend counts.

2. Annual aerial sex and age classifications.

3. Accurate sex and age information of hunter harvest.

4. Corrections of trend counts for animals not seen.

5. Annually updated harvest models predicting the effects of hunter harvest and wolf predation upon hunted ungulate herds.

6. Research models predicting effects of large-scale perturbations (wolves, fires, habitat alterations and acquisitions) upon ungulate herds.

An information rating index was used to quantify the information known on ungulates in the park area (Table 6). The index takes the form:

$$I = (D/(T*H))*100$$ where:

I= Index in percent
D= Total number of data categories filled from all herds of a species
T= Total number of data categories
H= Total number of herds of a species

Currently, elk have the highest information rating index of 58%. Mule deer are rated at 42%, bison at 29%, bighorn sheep at 28%, and moose at only 18%. Mountain goats and white-tailed deer were not rated because they are rare and inconsequential to wolf recovery.

Table 6. Research and inventory during the 1980's of the ungulate herd units located within or immediately adjacent to Yellowstone National Park.

Species Herd Unit	Annual Aerial Count	Annual Sex/ Age Classi-fica-tion	Cementum Annuli Aging of Harvests	Radio-telemetry Studies of Move-ments/ Distri-bution	Manage-ment Harvest Models	Sight-ability Corrected Pop. Est.	Pop. Est. by Harvest Model	Research Pop. Model(s)
Elk								
Gallatin	X	X		X				
Northern	X	X	'88/89	X		X		2 habitat; 2 wolf effects
Madison-Firehole	X	X		X				
Clarks Fork	X	X	X[a]	X	X		X	
North Fork Shoshone	X	X	X[a]	X	X		X	
Carter Mountain	X	X	X[a]		X		X	
Jackson	X	X		X	X		X	wolf effects
Sand Creek	X	X	1986-89	X				wolf effects
Bison								
Northern	X	X						wolf effects
Mary Mountain	X	X						
Pelican Valley	X	X						
Mountain Goats								
Absarokas	X	X						
Gallatin	X							
Palisades		X						
Moose								
Northern range	X	X		X		In progress		
Upper Gallatin								
Hebgen Lake								
Crandall								
Sunlight Basin								
North Fork Shoshone								
South Fork Shoshone								
Thorofare								
Jackson	X	X		X	X		X	
Targhee	X	X			X		X	
Falls River		X	Not annually	X[b]				
Big Bend		X		X				
Junipers		X		X				
Island Park		X		X				

Table 6. Continued.

Species Herd Unit	Annual Aerial Count	Annual Sex/ Age Classification	Cementum Annuli Aging of Harvests	Radio-telemetry Studies of Movements/ Distribution	Management Harvest Models	Sightability Corrected Pop. Est.	Pop. Est. by Harvest Model	Research Pop. Model(s)
Bighorn Sheep								
Spanish Peaks								
Taylor-Hilgards								
Cinnabar Mountain	X	X		X				
Tom Miner	X	X		X				
Mount Everts-Bear Creek	X	X						
Stillwater	X	X						
Rosebud	X	X		X				
Clarks Fork		X	X					
Trout Peak		X	X	X				
Wapiti Ridge		X	X	X				
Younts Peak		X	X					
Jackson	X	X					X	
Targhee	X	X					X	
Mule Deer								
Upper Gallatin								
Northern range	X	Partial						
South Fork Shoshone	X	X	X		X		X	
North Fork Shoshone	X	X	X		X		X	
Clarks Fork/ Sunlight	X	X	X		X		X	
Jackson	X	X			X		X	
Targhee	X	X			X		X	
Sand Creek		X	Prior to 1987					

[a] A sample of the harvest are aged.
[b] Movement studies by visual marking collars (Ritchie 1978).

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THE UNGULATE PREY BASE FOR WOLVES IN YELLOWSTONE NATIONAL PARK II. Elk, mule deer, white-tailed deer, moose, bighorn sheep, and mountain goats in areas adjacent to the park.

John A. Mack, P.O. Box 168, Yellowstone National Park, Wyoming 82190
Francis J. Singer, P.O. Box 168, Yellowstone National Park, Wyoming 82190
Mary E. Messaros, P.O. Box 168, Yellowstone National Park, Wyoming 82190

ABSTRACT: Statistics were compiled on ungulate populations in areas adjacent to Yellowstone National Park. A total of eight elk (Cervus elaphus) herds totaling 44,500-49,600 animals occupy the Yellowstone National Park area. From 1980 to 1988, an average of 31,000 and 18,500 elk summered and wintered in the park, respectively. Population estimates for seven elk herds increased an average of 38% (range 10%-67%) during the 1980s. Only one herd, the Madison Firehole herd, declined during this period. Harvests from 1980 to 1988 averaged 7,032 elk. Mule deer (Odocoileus hemionus) numbers from eight herds surrounding the park may exceed 20,500. Mule deer population estimates from all herds more than doubled during the 1980s. Some animals from each mule deer herd probably migrate into the park each summer. During the winter, less than 200 mule deer are counted within Yellowstone National Park. Two mule deer winter ranges abut the park boundary while six other winter ranges lie 16 km-48 km (10-30 miles) from the park boundary. Annual mule deer harvests averaged 3,236 from 1980 to 1988. Some of the increases in elk and mule deer population estimates can be attributed to improved methods in collecting population data. Because of these improvements, only data from 1980 to 1988 is reported (1989 data was unavailable). Few white-tailed deer (Odocoileus virginianus) summer and none winter within Yellowstone National Park. Gray wolf (Canis lupus) reintroduction is not predicted to affect white-tailed deer. Most moose (Alces alces) populations surrounding the park were stable during the 1980s except for the Jackson and Targhee herds which increased. Moose harvests averaged 545 annually. During the 1980s, two bighorn sheep (Ovis canadensis) populations increased, four remained stable, three declined, one crashed then partially recovered, and the trend of five others was unknown. Approximately 3,900 bighorns from 15 herds occupy winter range within 5 km-56 km (3-35 miles) of Yellowstone National Park. Bighorns from all 15 herds summer in or near the park. From 1980 to 1988, annual harvests averaged 130 legal (3/4-or-larger curl horn) rams. Less than 100 mountain goats (Oreamnos americanus) inhabit areas close to Yellowstone National Park. Hunting season regulations and restrictions varied widely for each big game species and state. All states had special archery seasons, primarily for elk and deer, which provided 2-4 weeks of hunting opportunity prior to the general rifle season. Montana and Wyoming tended to have the longest general rifle seasons, usually lasting a minimum of 1 month. Idaho general rifle seasons for elk and deer lasted only five days whereas seasons for moose lasted about two months.

Key Words: Elk, mule deer, white-tailed deer, moose, bighorn sheep, mountain goats, hunting seasons, harvests, population trends, Montana, Wyoming, Idaho.

INTRODUCTION

In August of 1988, Congress directed the National Park Service and the U. S. Fish and Wildlife Service to study several questions concerning gray wolf (Canis lupus) reintroduction into Yellowstone National Park. One question was "How a reintroduced population of wolves may affect the prey base in Yellowstone National Park and big game hunting in areas surrounding the park.". The first step in answering this question was to gather all the data on ungulates residing in the park, migrating into the park, or residing in areas adjacent to the park where wolves might prey upon them (Figs. 1 and 2). Additionally, the length of big game hunting seasons and the approximate numbers of hunters afield have implications on the future probability of incidental harvest of wolves.

This paper is the second (Singer 1990) in a series summarizing all available information on ungulates in and adjacent to Yellowstone National Park (Fig. 1). The first paper in this series dealt with elk,(Cervus elaphus) mule deer (Odocoileus hemionus), white-tailed deer, (Odocoileus virginianus) moose,(Alces alces) and pronghorn (Antilocapra americana) inhabiting the northern winter range of Yellowstone National Park and dealt with eight elk herds residing in or migrating into the park (Singer 1990, Fig. 2). The purpose of this paper is to present data on hunted ungulate herds residing adjacent to the park. Information concerning bison (Bison bison) populations from Yellowstone can be found in Meagher (1973, 1989). Information concerning bighorn sheep (Ovis canadensis) residing within the park can be found in Houston (1982) and R. Klukas (in prep.).

STUDY AREA

Yellowstone National Park

Nearly the entire area of Yellowstone National Park provides summer range for elk and limited range for other ungulates. The park is 79% forested. Lodgepole pine (Pinus contorta) grows at elevations between 2,300 m and 2,600 m (Houston 1982) and comprises about 81% of the forested area.

Winter snowfalls force elk and most other ungulates to leave the majority of the park area. Annual precipitation on the Pitchstone Plateau is 190 cm, most of which is snow. Other high plateaus and ridges (Two Ocean Plateau, Big Game Ridge, Madison Plateau, Chicken Ridge) receive nearly as much snowfall.

Northern Winter Range

Elk from the northern Yellowstone elk herd winter on Yellowstone's northern winter range. Houston (1982) described the area as about 100,000 ha in the Lamar and Gardner River drainages in the park and down the Yellowstone River valley to Dome Mountain in Montana. About 83% of the northern winter range

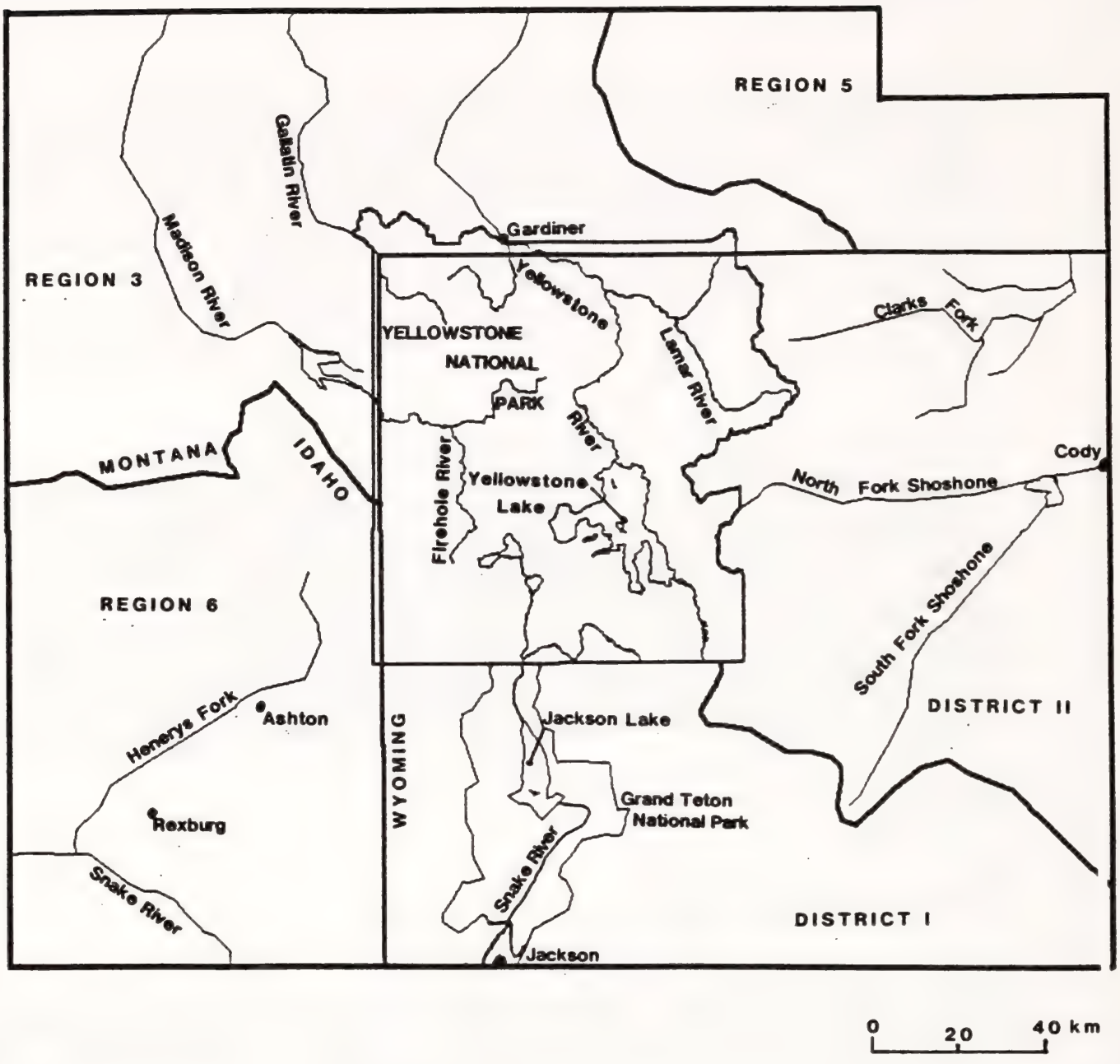


Fig. 1. Map of Yellowstone Park and 5 state game management regions included in this summary.

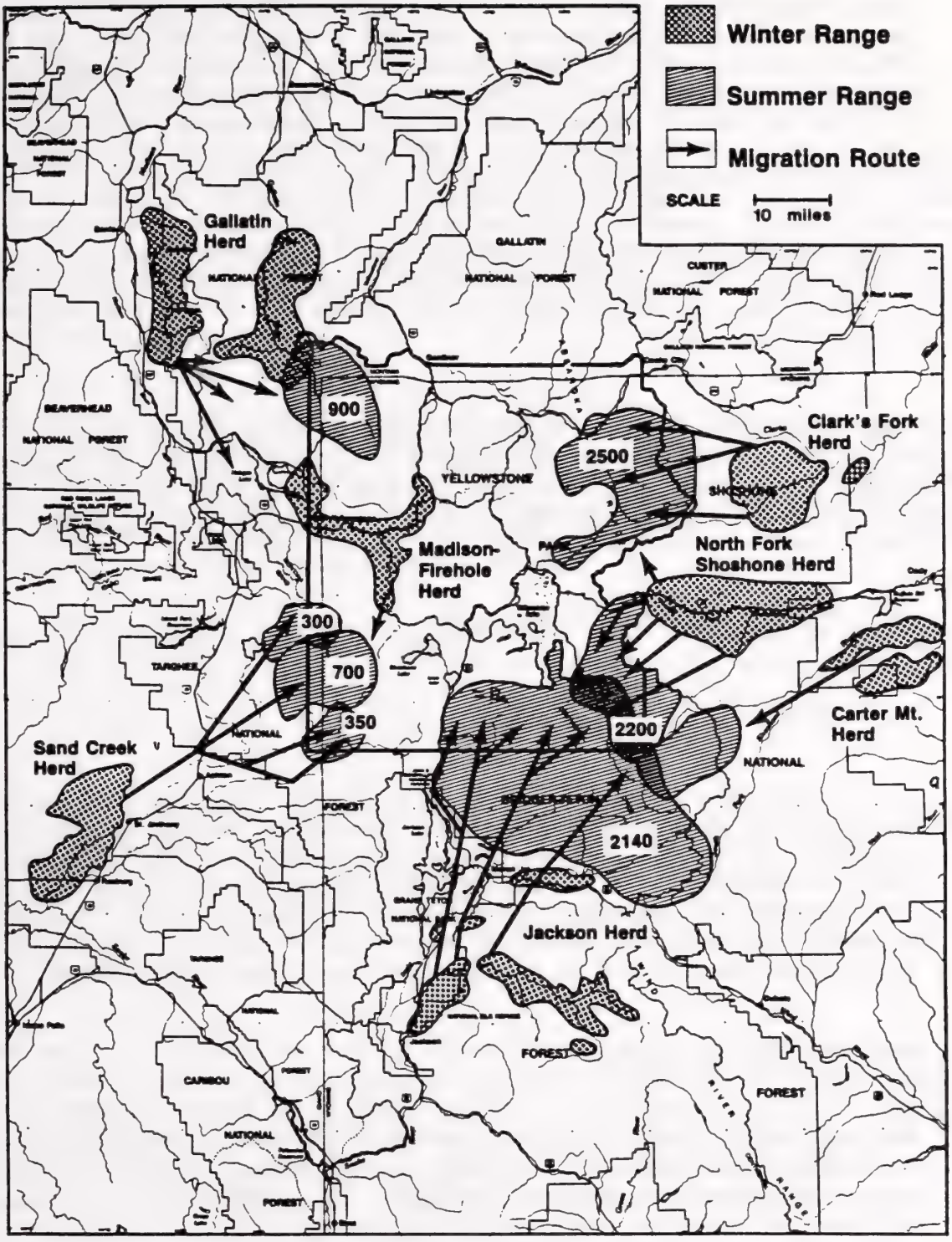


Fig. 2. Map showing the approximate winter ranges and those portions of summering areas within Yellowstone National Park for 7 elk herds other than the northern herd.

lies within the park and the remaining 17% lies on national forest and private lands outside the park. Elevations are lower (1,500 m to 2,400 m) than in the park interior, allowing more ungulates to winter in this area (Meagher 1973, Houston 1982). The northern winter range is somewhat warmer and drier than the rest of the park (Houston 1982) with total precipitation less than 75 cm (P. Farnes unpubl. data, Houston 1982). Mean annual precipitation decreases with elevation; 30 cm near Gardiner, Montana and 55 cm near the Lamar Ranger Station at a higher elevation.

North and Northwest of Yellowstone National Park

Gallatin Drainage

Over half of the 193 km (120 mi.)-long Gallatin River flows through mountains. Gallatin Canyon is characterized by broad open slopes and open Douglas-fir (Pseudotsuga menziesii) forests. Dense forests of spruce (Picea spp.), lodgepole pine, Douglas-fir, and aspen (Populus tremuloides) characterize the north facing slopes (Lovaas 1970, Taylor 1980).

East of Yellowstone National Park

Clarks Fork Drainage

The Clarks Fork river flows easterly through large intermountain valleys and steep grassy slopes on the eastern foothills. Mountain types vary from sedimentary strata of the Beartooths northeast of the drainage to the igneous Absaroka Mountains to the southeast. Open parks and long grass-covered ridges and plateaus provide excellent elk spring/summer range. Rugged forests and limited riparian habitat characterize moose habitat in this area. Much of this area is wilderness and is in the Shoshone National Forest.

North Fork Shoshone Drainage

The North Fork Shoshone, an 80-km-long (50 mi.) east-west river valley in the Shoshone National Forest, is deeply incised and eroded with towering igneous rock formations (Hurley et al. 1988). This upper valley is heavily timbered and broadens into an arid basin, the Wapiti Valley. Private and Bureau of Land Management lands comprise the Wapiti Valley's juniper-covered (Juniperus spp.) dry foothills and rock outcrops.

South Fork Shoshone Drainage

The South Fork valley is wide and arid at its eastern end and grades into grassy rolling hills and juniper-covered foothills at the western end. Riparian areas are primarily located on private land.

South of Yellowstone National Park

Snake River Drainage

A large intermountain basin, Jackson Hole, is surrounded by the mountains of Yellowstone National Park and the Teton Wilderness to the north, the Teton Range to the west, and the Gros Ventre Range to the east. Spruce and subalpine fir (Abies lasiocarpa) and tall forb meadows dominate the mountains. Cottonwood (Populus angustifolia) and willow (Salix spp.) occupy the large wide riparian corridors of the Snake River, Buffalo River, Spread Creek, Pacific Creek, and Gros Ventre River.

Steep narrow drainages running east and west across the Wyoming-Idaho border characterize the Teton Range. Steep rocky peaks, alpine meadows, subalpine fir and lodgepole pine forests, willow bottoms along stream courses, and aspen-conifer habitats characterize this area. During the winter, Pacific storm fronts result in heavy snowfalls in the Teton Range, which is in the Targhee National Forest and Grand Teton National Park.

Southwest of Yellowstone National Park

Idaho

The Island Park area is a large volcanic caldera about 29 km by 37 km in size. Elevation of the basin floor is 1,800 m-2,000 m. Lodgepole pine forests cover about 80% of the area. The Big Bend Ridge area has elevations to 2,100 m. This area consists of 27% Douglas-fir, 20% lodgepole, 26% aspen, and 24% shrubland (Ritchie 1978). These areas have a temperate climate with long winters and deep snow.

Southwest of the Island Park and Big Bend Ridge areas is the Sand Creek-Junipers winter range. Sand Creek, at 1,500 m elevation, provides nearly all the winter range for elk, mule deer and a single moose population. This arid range, 32 km (20 mi.) from any forested area, is characterized by lava flows overlain by sand dunes. Vegetation types are interspersed sagebrush (Artemisia spp.)/bunchgrass and grasslands. Snow depths commonly exceed 61 cm.

MONTANA SUMMARIES

Hunting Season Regulations

The following is a brief summary describing hunting seasons for Montana hunting districts adjacent to Yellowstone National Park. All elk, deer, and moose hunting districts are under jurisdiction of Region 3 (headquarters in Bozeman) of the Montana Department of Fish, Wildlife, and Parks. Bighorn sheep hunting

areas adjacent to the park are located in both Region 3 and Region 5 (headquarters in Billings). For the Montana summaries, all hunting districts for all species (Fig. 3,4, and 5) were assigned a hunting area name (Table 7).

Elk

Most areas had special archery seasons which began the first week in September and lasted until the second week in October. During archery season, either-sex elk could be legally taken.

General rifle season began the third or fourth week of October and ended the last week in November. Since 1981, opening day has been during the fourth week in October. Only antlered bulls could be taken during the general season.

Special Permits

Since 1982, an average of 1336 special permits (antlerless or either-sex) from five areas were available each year for hunts during the general season. A sharp increase in the number of permits available began in 1984 (Fig. 6). Yellowstone River-West (district 314) and East Madison (district 362) contributed the bulk of this increase. These permits were designed primarily to harvest antlerless elk. An average of 4101 either-sex permits (from 2 to 3 districts) were available each year for a late season hunt from mid-December to February the following year (Fig. 7). Since 1981 the number of late season permits available has remained relatively constant.

Deer

Mule and white-tailed deer can be harvested in nearly all hunting areas in Montana adjacent to Yellowstone National Park. However, white-tailed deer make up a small percentage of the harvest in these hunting areas. Special archery season began the first week in September and lasted until mid-October. During archery season, both sexes of either species could be harvested.

The general season opened between the third and fourth week in October and closed the end of November (the same as the general elk season). During the general season, all districts allowed only antlered bucks to be harvested. In 1985, however, three of six districts expanded the harvest to allow either-sex white-tailed deer to be taken.

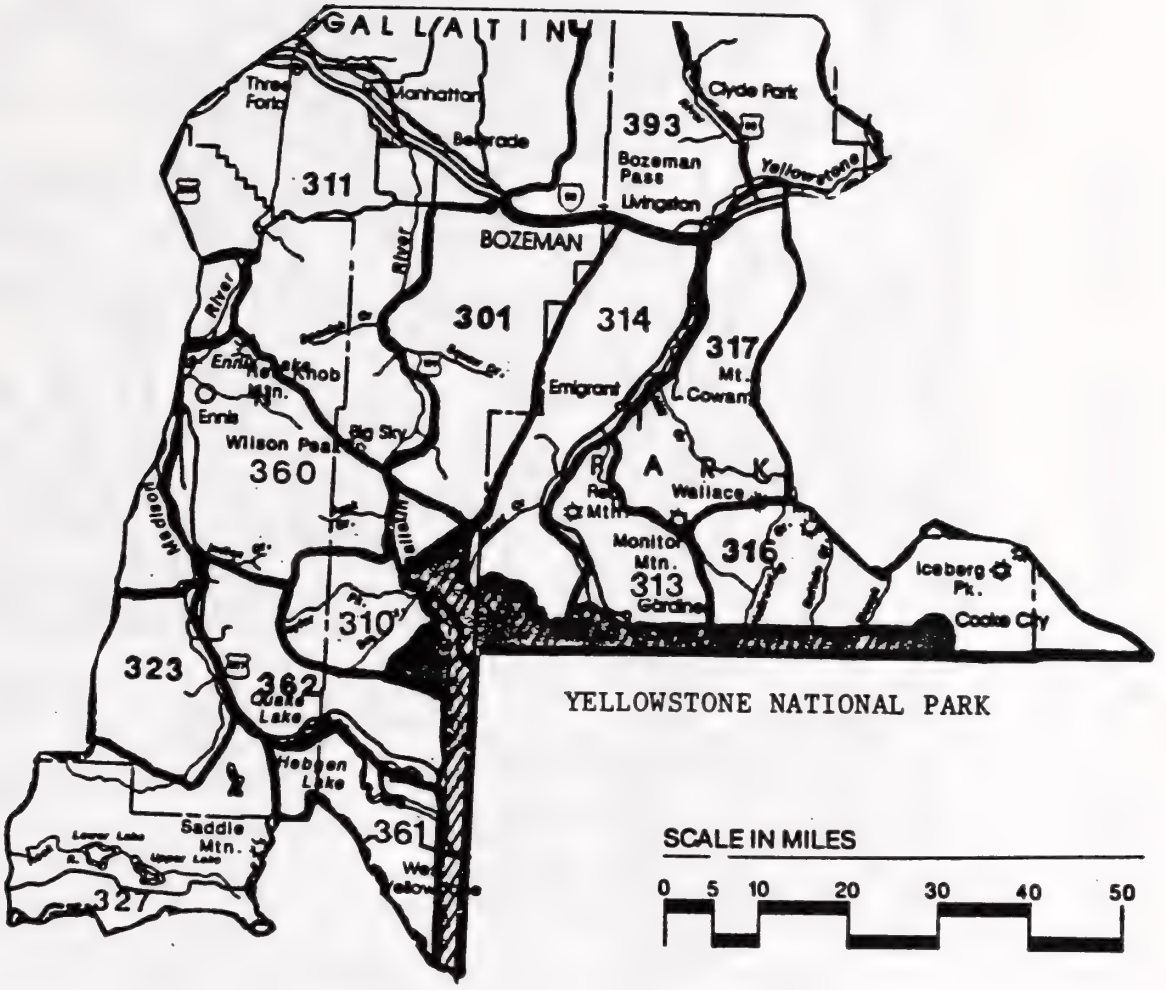


Fig. 3. Boundaries of elk and deer hunting districts in Montana adjacent to Yellowstone Park.

Fig. 4. Boundaries of moose hunting districts in Montana adjacent to Yellowstone Park.

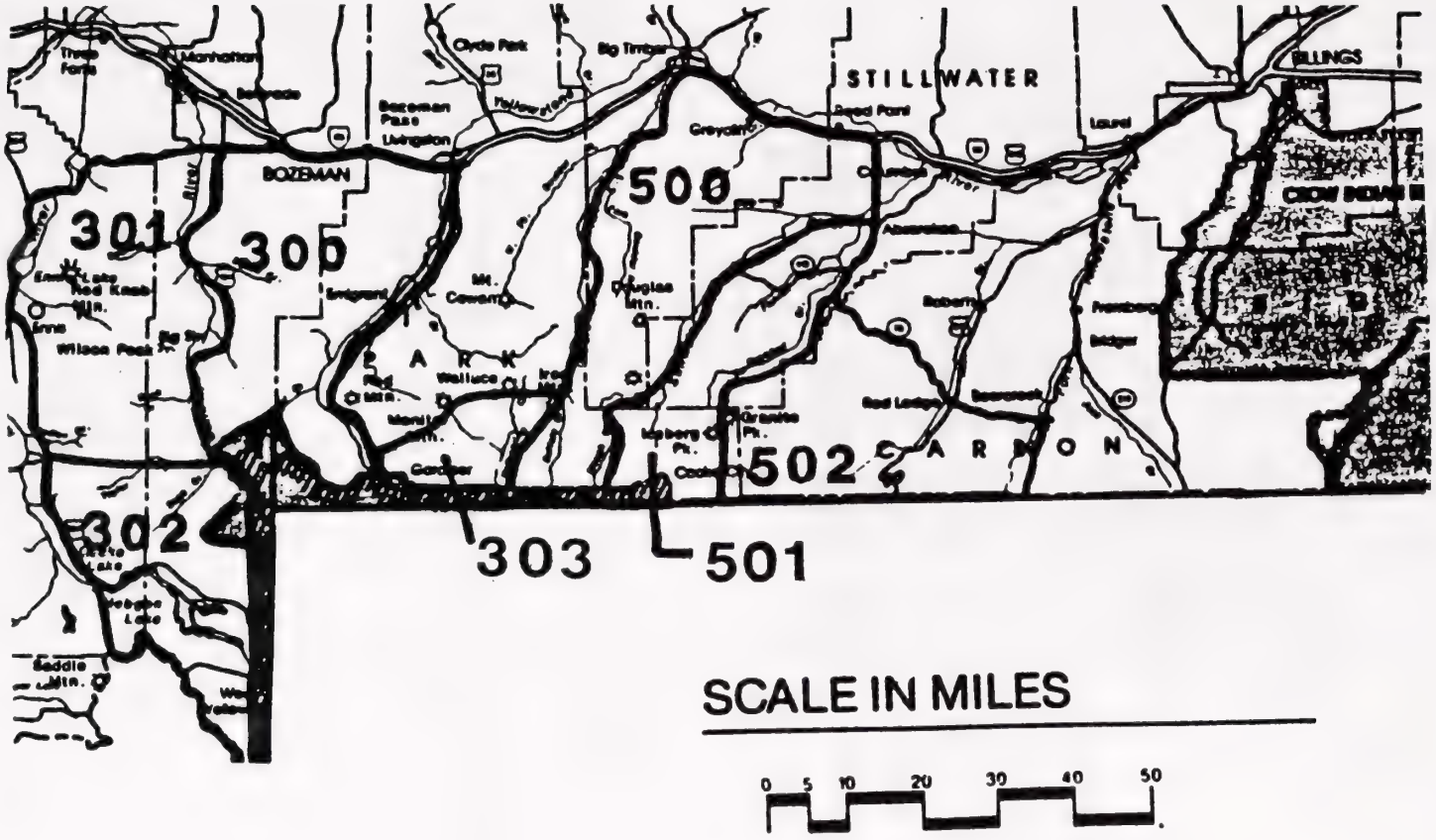


Fig. 5. Boundaries of bighorn sheep hunting districts in Montana adjacent to Yellowstone Park.

Table 7. Montana hunting areas and their associated hunting districts bordering Yellowstone National Park.

Big game Species	Hunting Area	Hunting District(s)
Elk and deer	Upper Gallatin	310
	Yellowstone River-East	313
	Yellowstone River-West	314
	Hellroaring	316
	Hebgen Lake	361
	East Madison	362
Moose	Gallatin Canyon	306, 307, 310
	Upper Yellowstone	314
	Hellroaring	316
	Buffalo Fork	317
	Slough Creek	318
	Upper Stillwater	322
	Eagle/Bear Creeks	328
	Hebgen	309, 361
Bighorn sheep	Gallatin/Yellowstone	300
	Spanish Peaks	301
	Taylor/Hilgards	302
	Absaroka	303
	Stillwater	500
	Rosebud	501

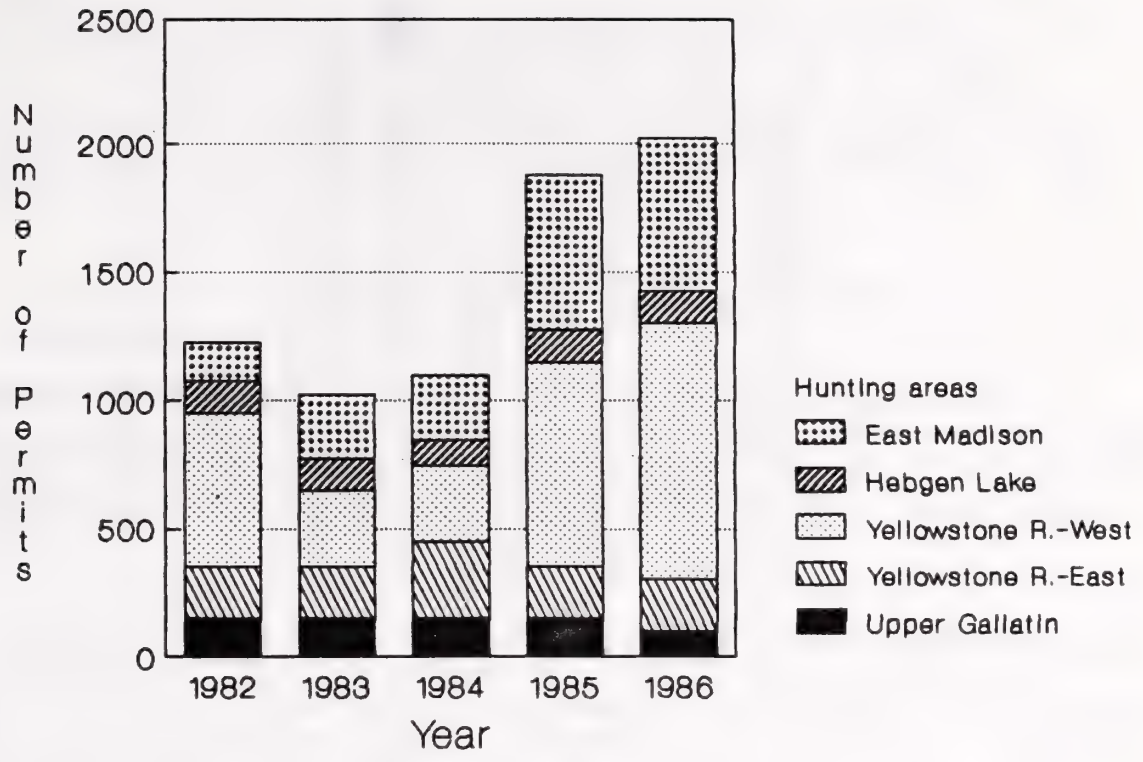


Fig. 6. Number of special elk permits (either-sex or antlerless) offered in 5 hunting areas in Montana north of Yellowstone National Park, 1982-1986.

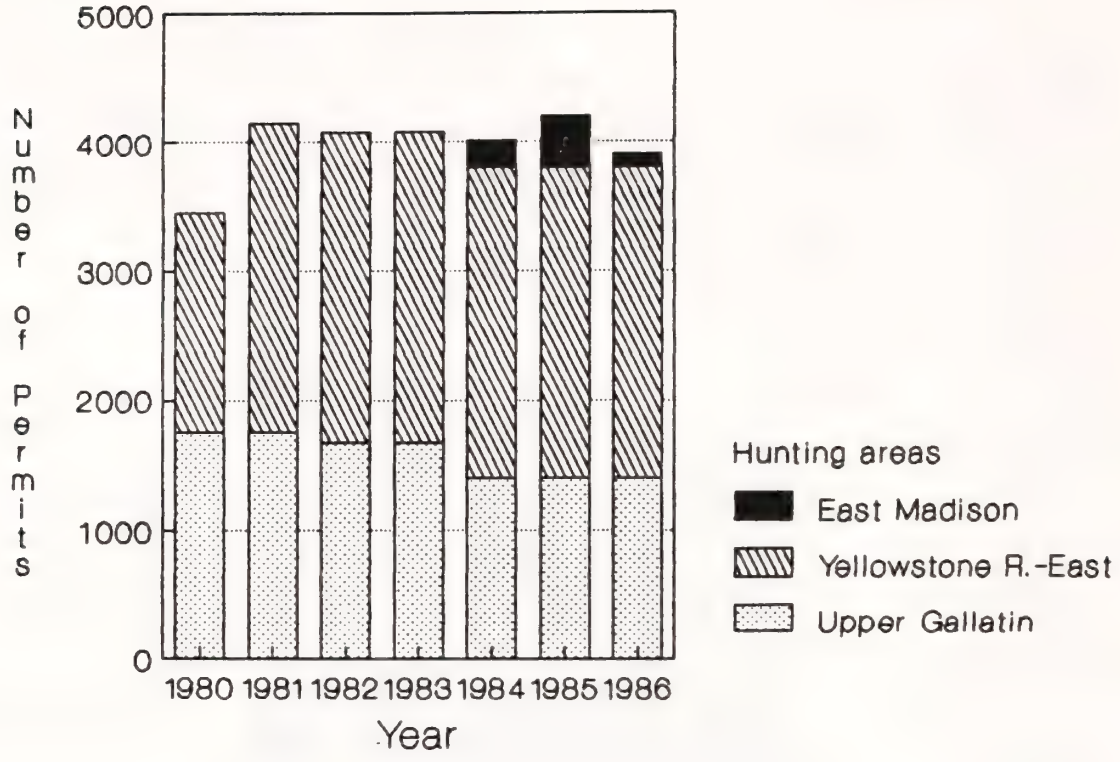


Fig. 7. Number of late season special elk permits (either-sex or antlerless) offered for 3 hunting areas in Montana north of Yellowstone Park, 1980-86.

Special Permits

An average of 806 antlerless either species deer tags and/or permits were available each year in three out of six districts since 1982 (Fig. 8). The number of antlerless permits has increased since 1980. The largest contributor to this increase was Yellowstone River-West (district 314). Reducing the number of does in the population was the apparent objective. Hellroaring and Hebgen Lake areas (districts 316 and 361, respectively) have not had any special permits since 1980.

Moose

Obtaining a special permit is the only way to legally hunt moose in Montana. In 1980 and 1981, opening day was September 15 or the third week in October (depending upon the district). In 1982, opening day changed to September 15. Since 1980, closing day has been between November 25 and December 1.

For most districts bordering the park, either-sex and antlered bull permits were available (Fig. 9). An average of 90 and 48 antlered bull and either-sex permits, respectively, were available each year. The ratio of antlered bull to either-sex permits ranged from 1.5:1 to 3:1. No district offered more than 25 total permits during the year.

Between 1980 and 1985, only antlered bull permits were available in Buffalo Fork (district 317). In 1986, four antlerless permits were also offered. A portion of the Gallatin Canyon area and Eagle/Bear Creeks (districts 307 and 328, respectively) were created in 1984 and an average of eight antlered bull permits were available each year. District 307 also provided two either-sex permits a year.

Bighorn Sheep

A separate permit is required for hunting bighorn sheep. No special archery season exists for hunting bighorn sheep. All districts had an unlimited number of permits (no drawing) available and the bighorn sheep harvest was regulated by quotas. When quotas were reached, the season for unlimited license holders was closed. Seasons for unlimited license holders opened on September 1 or 15 and closed the first or last week in November if quotas were not reached sooner. Typically, the quotas were reached and seasons closed before the scheduled closing date.

During 1980 and 1981, the Gallatin/Yellowstone and Absaroka areas (districts 300 and 303, respectively) offered additional permits through a drawing. The Stillwater area (district 500) offered more drawing permits in 1983 and 1984. After 1984, only district 300 offered any additional drawing permits. Permits obtained through a drawing had opening dates

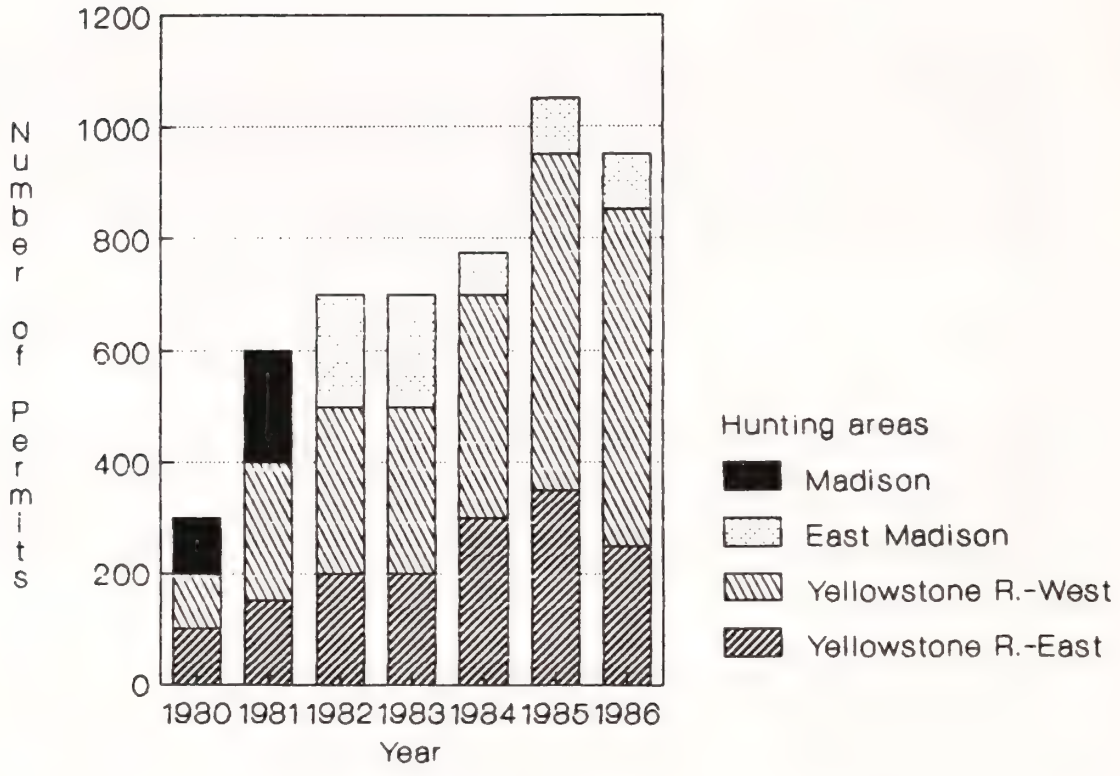


Fig. 8. Number of special deer permits (antlerless-either species) offered in 4 Montana hunting areas north of Yellowstone Park, 1980-86. The Madison area (district 360) was split into 2 districts (360 and 362) in 1982 with the East Madison (362) currently bordering the Park.

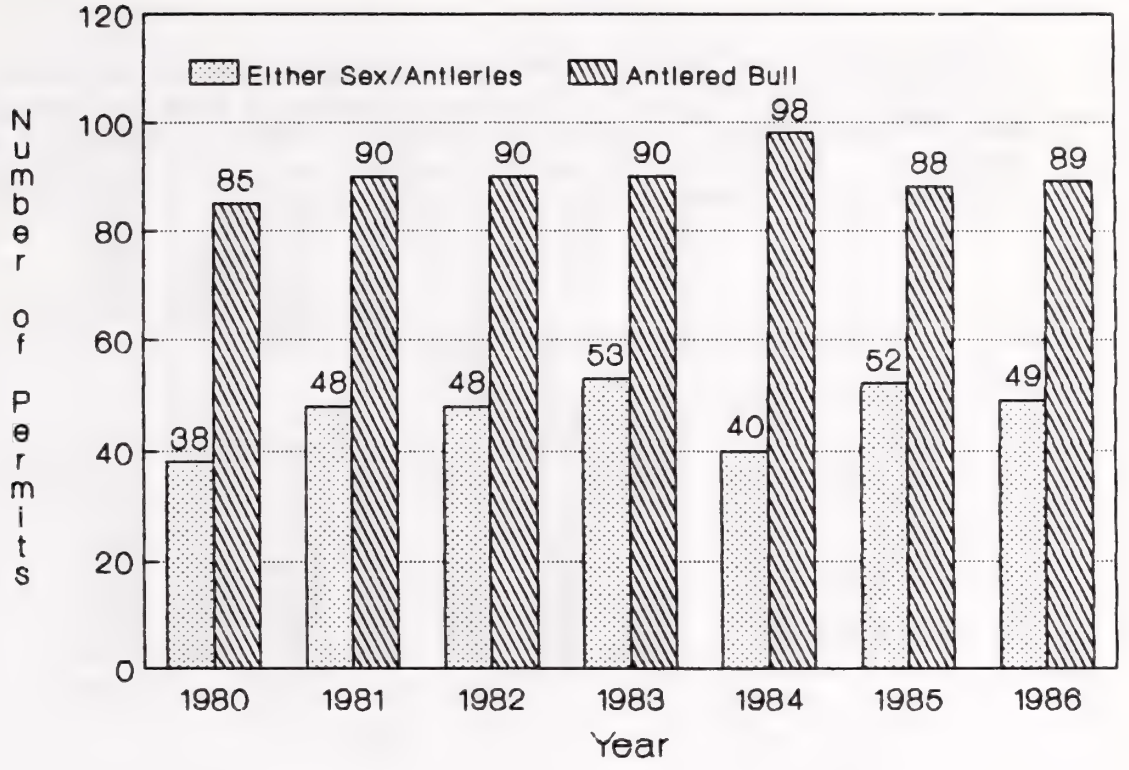


Fig. 9. Number of moose permits offered for the Gallatin Canyon (districts 306, 307, and 310), Upper Yellowstone (314), Hellroaring (316), Buffalo Fork (317), Slough Creek (318), Eagle/Bear Creeks (328), Hebgen Lake (309) and 361), and Upper Stillwater (322) hunting areas in Montana north of Yellowstone Park, 1980-1986.

during the first week in November (after the unlimited season closed) and closing dates between November 27 and December 11.

Bighorn sheep unlimited license quotas averaged 22 per year in six districts (Fig. 10) and the average number of hunters purchasing licenses was 485/year (Fig. 10 and 11). Between 1980 and 1986, the quotas steadily declined. The number of hunters purchasing licenses declined from 1980 to 1985 but 1986 showed a large increase (Fig. 11).

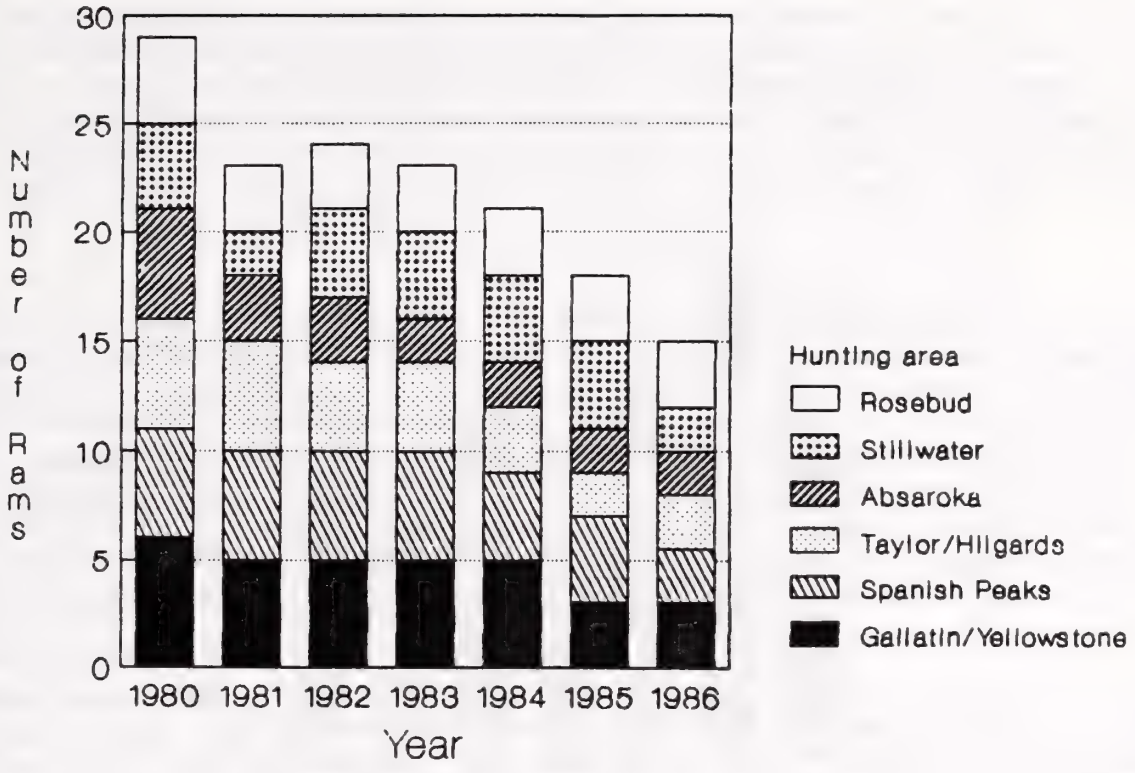


Fig. 10. Bighorn sheep quotas (for harvest with an unlimited license) for 6 Montana hunting areas located north of Yellowstone Park, 1980-86.

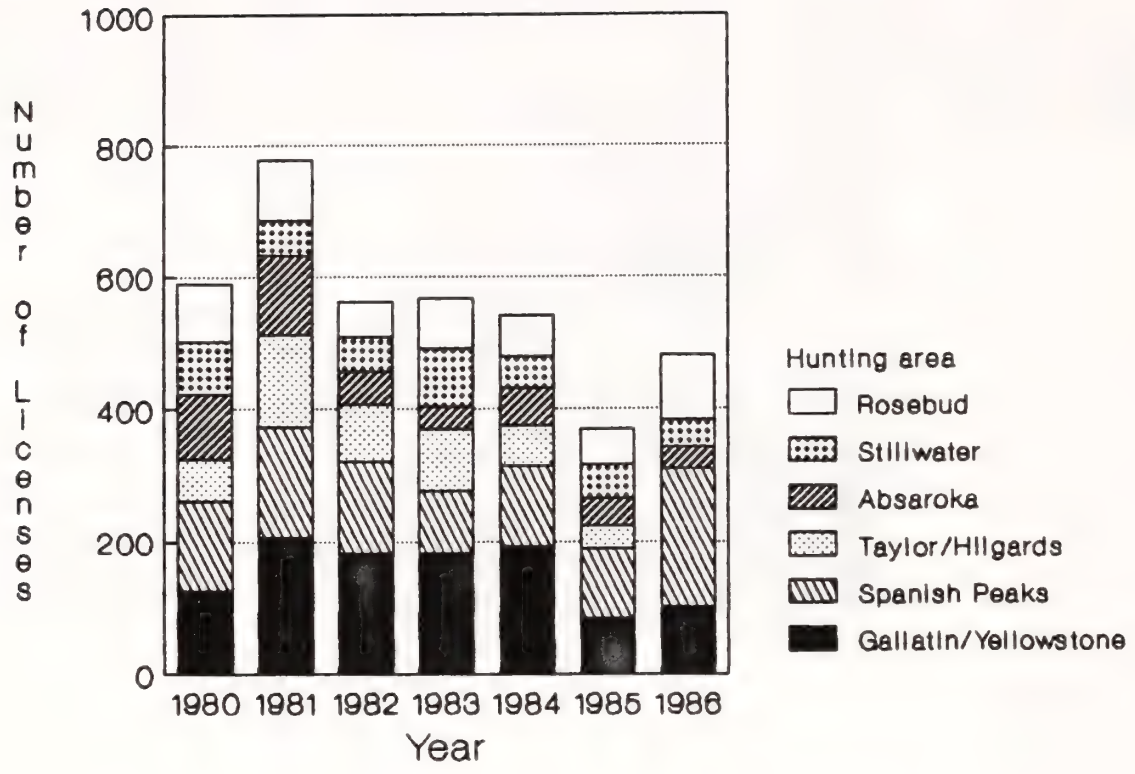


Fig. 11. Number of unlimited licenses sold for 6 Montana hunting areas located north of Yellowstone Park, 1980-86. In 1986, the Spanish Peaks (district 301) and Taylor/Hilgards (302) areas had a combined quota of 5 rams and the number of permits sold were valid for both areas. Therefore, the total permits sold are included only under the Spanish Peaks area.

Harvest Summaries

The harvest summaries represent an estimate of the number of animals harvested. Much of the deer and elk harvest information was gathered from statewide telephone surveys of approximately 40% of the hunters. Special permit harvest reports (deer, moose, bighorn sheep) probably closely reflect the actual numbers of individuals harvested. Elk harvests for Montana are presented in Singer (1989).

Deer

From 1980 to 1986, an average of 1,762 deer were killed each year (Table 8). Although the number of bucks taken each year declined, the number of antlerless deer taken rose, resulting in a relatively stable yearly harvest since 1981 (Table 9, Fig. 12). From 1980 to 1986, a yearly average of 82.6% of the total deer harvested from areas adjacent to Yellowstone National Park came from Yellowstone River-East and West (districts 313 and 314, respectively). An average of 91% of the annual harvest consisted of mule deer (69% antlered, 22% antlerless). An average of 6% of the annual harvest consisted of antlered white-tailed deer while 3% consisted of antlerless white-tailed deer (Fig. 13).

Moose

The moose harvest remained relatively constant between 1980 and 1986 averaging 114 animals/year for seven areas (Table 10, Fig. 14). Percent success also remained constant averaging 84% per year. The majority of the harvest was bulls (75% per year) with cows (17% per year) and calves (8% per year) contributing the remainder.

Bighorn Sheep

The unlimited license harvest from six areas bordering the park averaged 16 bighorns/year between 1980 and 1986. Hunter success for unlimited license holders was low, erratic, and averaged 4.9% per year (Table 11, Fig. 15). The yearly quota and the number of hunters purchasing licenses influenced hunter success for unlimited license hunters. Hunters who obtained a license through a drawing harvested an average of nearly four bighorns/year. Success for these individuals was higher, averaging 87.3% per year.

Table 8. Mule and whitetail deer harvest in Montana for districts adjacent to northern Yellowstone National Park, 1980-1986 (from Foss 1981-1987).

Year	Hunting District	Number of Hunters	Mule Deer		Whitetail Deer		Total	Percent Success[a]
			Antlered	Antlerless	Antlered	Antlerless		
1980	310	684	82	0	8	0	90	13
	313	849	223	26 (5 Unk.)	8	3	265	31
	314	1711	556	53 (13 Unk.)	60	5	687	40
	316	539	91	0	0	0	91	17
	361	221	36	0	3	0	39	18
1981	310	627	85	0 (4 Unk.)	12	0	101	16
	313	927	450	47 (7 Unk.)	34	12(1 Unk.)	551	59
	314	1621	904	94 (10 Unk.)	41	6(1 Unk.)	1055	65
	316	308	83	0 (6 Unk.)	0	0	89	29
	361	311	85	0	0	0	85	27
1982	310	485	78	0 (5 Unk.)	5	0	88	18
	313	1123	465	101 (5 Unk.)	41	2(1 Unk.)	615	55
	314	1683	508	111 (5 Unk.)	44	6	674	40
	316	308	47	0	5	0	52	17
	361	224	48	0 (9 Unk.)	8	0	65	29
	362[a]	320	90	23 (6 Unk.)	0	5	124	39
1983	310	318	84	0	9	0	93	29
	313	1368	549	197	6	5	757	55
	314	1827	625	216	99	35	975	53
	316	256	40	0	15	0	55	21
	361	124	25	0	9	0	34	27
	362	488	32	64	6	6	108	22
1984	310	398	59	0	12	0	71	18
	313	1102	341	239	6	6	592	54
	314	1941	625	323	80	54	1082	56
	316	121	42	0	0	0	42	35
	361	189	26	0	6	0	32	17
	362	377	61	20	0	13	94	25
1985	310	398	100	0	14	0	114	29
	313	910	242	215	5	35	497	55
	314	1978	670	322	101	80	1172	59
	316	203	46	0	0	0	46	23
	361	110	17	0	0	0	17	15
	362	333	99	38	0	12	149	45
1986[b]	310	312	49	0	4	8	61	19
	313	922	337	151	16	15	519	50
	314	1278	518	315	64	69	966	61
	316	203	44	4	0	8	56	25
	361	—	20	0	4	0	24	—
	362	—	40	48	8	8	104	—

[a] Prior to 1982 district 362 did not exist and harvest summaries are not possible.
[b] In 1986, percent success was measured as percent of hunters taking one or more deer.

Table 9. Antlerless harvest and hunter success for Montana districts having either species deer B tags.

Year	Hunting District	No. Permits/ No. Hunters	Number of		Number of		Percent Success[a]
			Does	Fawns	Mule Deer	Whitetail Deer	
1986	313	250/---	---	---	132	5	55
	314	600/---	---	---	291	28	53
	362[b]	100/---	---	---	36		36
1985	313	350/272	218	4	196	26	82
	314	600/511	352	17	305	60	71
	362	100/76	40	0	33	7	53
1984	313	350/283	237	8	239	6	86
	314	600/498	374	3	323	54	76
	362	100/68	33	0	26	13	47
1983	313	300/300	196	6	197	5	67
	314	400/400	248	3	216	35	63
	362[c]	300/300	70	0	64	6	23
1982[d]	313	200/168	103	0	101	2	79
	314	300/219	107	0	101	6	64
	362[c]	200/105	27	0	23	5	42
1981	313[c,f]	200/143	48	1	47(3 Unk.)	2(1 Unk)	34[e]
	313[f]	50/24	7	1	0	8	33
	314[c]	400/290	94	6	94(6 Unk.)	6	37[e]
1980	313[c]	100/80	29	0	26(2 Unk.)	3	39[e]
	314[c]	200/156	51	7	53(1 Unk.)	5	38[e]

[a] Percent success measured as success/license in 1986.
[b] Permits valid only for mule deer does.
[c] Special permit allowing kill of antlered or antlerless deer valid only with the A tag license.
[d] In this survey a number of bucks were reported as being killed on the B tag license. These are not reported here although the percent success will reflect the total number of deer (bucks and does) killed.
[e] Although bucks were reported as being taken by individuals holding special permits, percent success is measured only as the number of antlerless deer (plus unknowns) taken/number of hunters.
[f] B tags for taking antlerless white-tailed deer only.

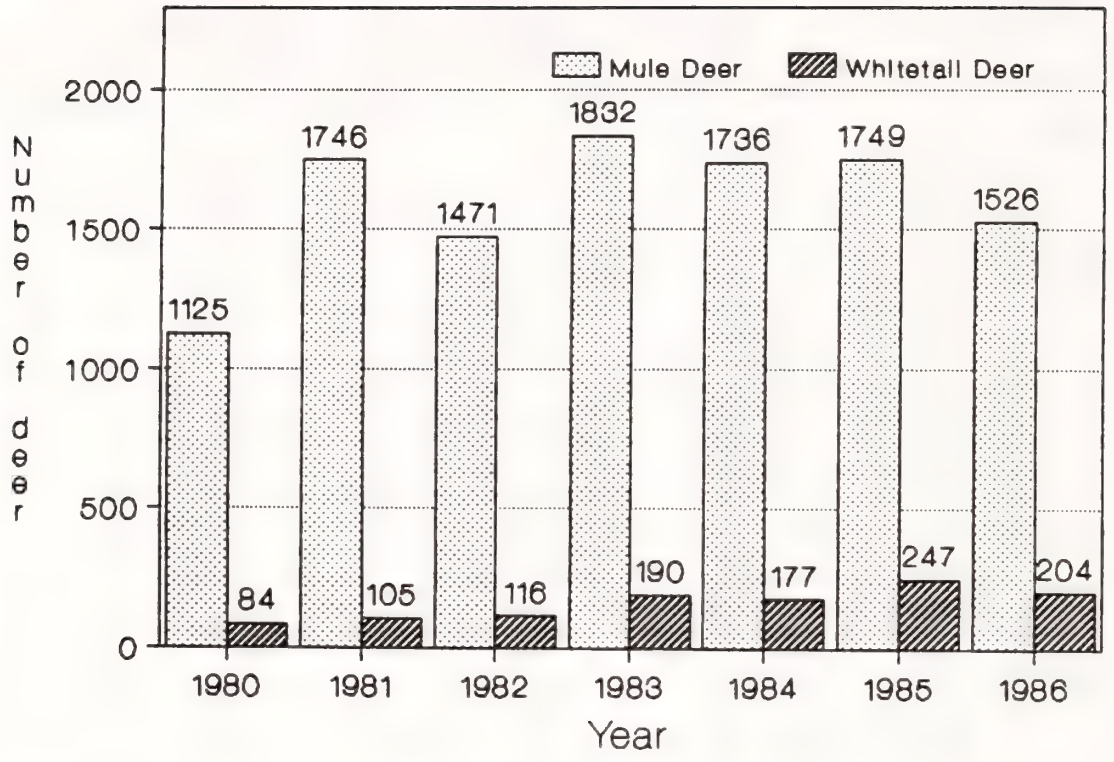


Fig. 12. Number of mule and whitetail deer harvested from the Upper Gallatin (district 310), Yellowstone River-East (313), Yellowstone River-West (314), Hellroaring (316), Hebgen Lake (361), and East Madison (362) areas of Montana north of Yellowstone Park, 1980-86. Harvests from the East Madison were not included until 1982.

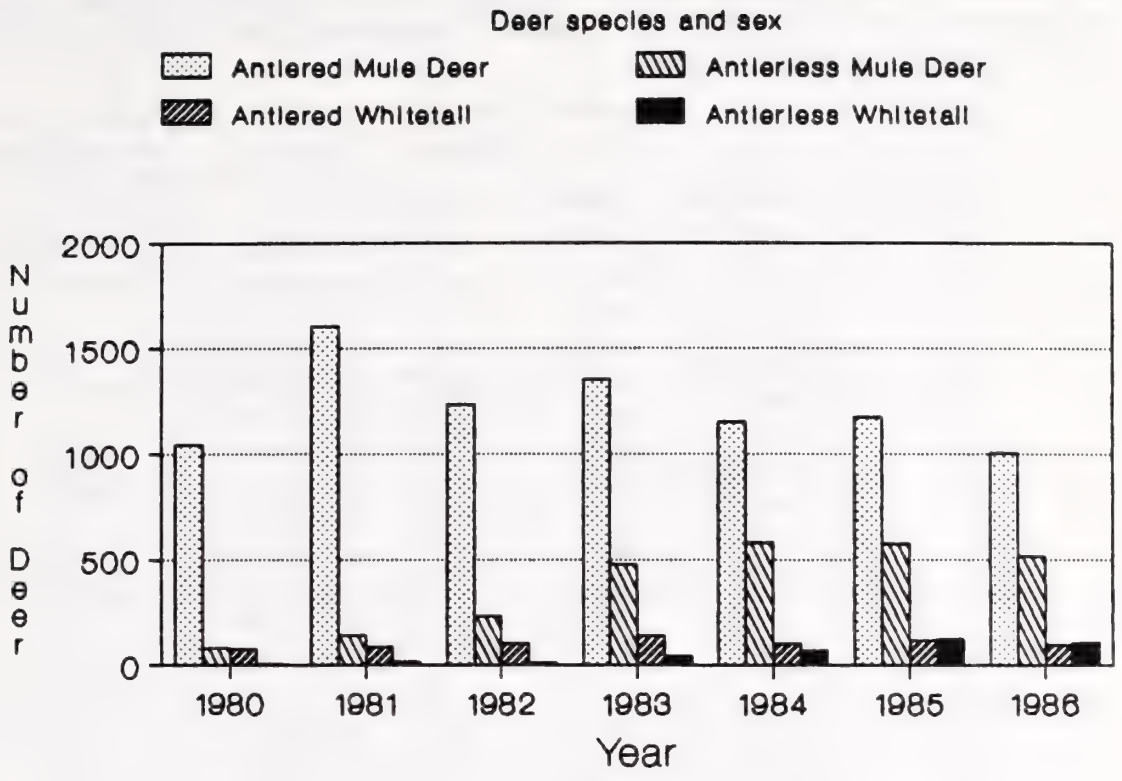


Fig. 13. Breakdown of deer harvest according to species and sex for the Upper Gallatin (district 310), Yellowstone River-East (313), Yellowstone River-West (314), Hellroaring (316), Hebgen Lake (361), and East Madison (362) hunting areas of Montana north of Yellowstone Park, 1980-1986. Harvests from the East Madison were not included until 1982.

Table 10. Moose harvest survey results showing sex and age composition, number of hunters, and percent hunter success for hunting districts adjacent to Yellowstone National Park in Region 3, Montana, 1980-1986 (from Alt and Foss 1987, Swenson and Foss 1986).

Year	Hunting District	Number of Permits	Number of Hunters	Percent Success	Sex and age composition[a]			Total Harvest
					Bulls	Cows	Calves	
1980	306	3 Either-sex	3	67	1	0	1	2
		10 Antlered	10	60	6	0	0	6
	309	5 Either-sex	5	100	2	2	2	6
		15 Antlered	15	60	9	0	0	9
	310	5 Either-sex	5	100	3	2	0	5
		10 Antlered	10	100	10	0	0	10
	314	5 Either-sex	5	60	0	2	1	3
		15 Antlered	15	40	5	0	1	6
	316	5 Either-sex	5	80	2	2	0	4
		5 Antlered	5	20	1	0	0	1
	317	5 Antlered	5	60	3	0	0	3
	318	10 Either-sex	10	80	7	1	0	8
	322	5 Either-sex	5	60	0	1	1	3[b]
		10 Antlered	10	30	3	0	0	3
	361	10 Either-sex	10	100	5	3	3	10[b]
		15 Antlered	15	80	13	0	0	13
1981	306	3 Either-sex	3	100	2	2	0	4
		10 Antlered	9	78	7	0	0	7
	309	5 Either-sex	5	100	1	3	1	5
		15 Antlered	14	100	13	1	0	14
	310	10 Either-sex	10	100	5	6	0	10
		10 Antlered	10	70	7	0	0	7
	314	5 Either-sex	5	100	3	2	0	5
		15 Antlered	14	71	10	0	0	10
	316	5 Either-sex	5	80	3	1	0	4
		5 Antlered	2	100	2	0	0	2
	317	5 Antlered	5	100	5	0	0	5
	318	5 Either-sex	5	80	2	2	0	4
		5 Antlered	5	40	2	0	0	2
	322	5 Either-sex	5	100	3	2	0	5
		10 Antlered	9	67	6	0	0	6
	361	10 Either-sex	10	100	4	6	0	10
		15 Antlered	14	93	13	0	1	14
1982	306	3 Either-sex	3	100	2	1	0	3
		10 Antlered	9	78	7	0	0	7
	309	5 Either-sex	5	100	5	0	0	5
		15 Antlered	15	100	14	0	1	15

Table 10. Continued.

Year	Hunting District	Number of Permits	Number of Hunters	Percent Success	Sex and age composition[a]			Total Harvest
					Bulls	Cows	Calves	
1982	310	15 Either-sex	15	100	11	4	0	15
		15 Antlered	15	100	15	0	0	15
	314	5 Either-sex	5	100	3	1	1	5
		15 Antlered	14	64	9	0	0	9
	316	5 Either-sex	5	80	1	3	0	4
		5 Antlered	5	80	4	0	0	4
	317	5 Antlered	5	100	5	0	0	5
	318	5 Either-sex	3	100	2	2	0	3
		5 Antlered	5	100	3	0	2	5
	322	5 Either-sex	5	60	2	0	2	4
		10 Antlered	10	90	9	0	0	9
	361	10 Either-sex	10	100	3	7	0	10
		15 Antlered	15	93	12	0	1	14
1983	306	3 Either-sex	3	100	3	0	0	3
		10 Antlered	10	80	8	0	0	8
	309	5 Either-sex	5	100	3	2	0	5
		15 Antlered	14	93	13	0	0	13
	310	15 Either-sex	15	93	7	6	1	14
		10 Antlered	10	80	8	0	0	8
	314	5 Either-sex	5	80	3	1	0	4
		15 Antlered	12	17	2	0	0	2
	316	2 Either-sex	2	100	2	0	0	2
		5 Antlered	5	60	3	0	0	3
	317	5 Antlered	5	60	3	0	0	3
	318	5 Either-sex	5	80	1	2	1	4
		5 Antlered	5	100	5	0	0	5
	322	5 Either-sex	5	100	3	1	1	5
		10 Antlered	10	100	10	0	0	10
	361	10 Either-sex	10	100	3	5	0	10
		15 Antlered	15	93	14	0	0	14
1984	306	5 Either-sex	3	100	0	3	0	3
		10 Antlered	10	100	9	0	1	10
	307	5 Antlered	5	100	5	0	0	5
	309	5 Either-sex	5	100	4	0	1	5
		15 Antlered	12	75	9	0	0	9
	310	10 Either-sex	9	100	6	3	0	9
		15 Antlered	15	80	12	0	0	12
	314	10 Antlered	9	100	8	0	1	9
	316	2 Either-sex	1	100	1	0	0	1
		5 Antlered	4	100	4	0	0	4
	317	5 Antlered	4	75	3	0	0	3

Table 10. Continued.

Year	Hunting District	Number of Permits	Number of Hunters	Percent Success	Sex and age composition[a]			Total Harvest
					Bulls	Cows	Calves	
1982	310	15 Either-sex	15	100	11	4	0	15
		15 Antlered	15	100	15	0	0	15
	314	5 Either-sex	5	100	3	1	1	5
		15 Antlered	14	64	9	0	0	9
	316	5 Either-sex	5	80	1	3	0	4
		5 Antlered	5	80	4	0	0	4
	317	5 Antlered	5	100	5	0	0	5
	318	5 Either-sex	3	100	2	2	0	3
		5 Antlered	5	100	3	0	2	5
	322	5 Either-sex	5	60	2	0	2	4
		10 Antlered	10	90	9	0	0	9
	361	10 Either-sex	10	100	3	7	0	10
		15 Antlered	15	93	12	0	1	14
1983	306	3 Either-sex	3	100	3	0	0	3
		10 Antlered	10	80	8	0	0	8
	309	5 Either-sex	5	100	3	2	0	5
		15 Antlered	14	93	13	0	0	13
	310	15 Either-sex	15	93	7	6	1	14
		10 Antlered	10	80	8	0	0	8
	314	5 Either-sex	5	80	3	1	0	4
		15 Antlered	12	17	2	0	0	2
	316	2 Either-sex	2	100	2	0	0	2
		5 Antlered	5	60	3	0	0	3
	317	5 Antlered	5	60	3	0	0	3
	318	5 Either-sex	5	80	1	2	1	4
		5 Antlered	5	100	5	0	0	5
	322	5 Either-sex	5	100	3	1	1	5
		10 Antlered	10	100	10	0	0	10
	361	10 Either-sex	10	100	3	5	0	10
		15 Antlered	15	93	14	0	0	14
1984	306	5 Either-sex	3	100	0	3	0	3
		10 Antlered	10	100	9	0	1	10
	307	5 Antlered	5	100	5	0	0	5
	309	5 Either-sex	5	100	4	0	1	5
		15 Antlered	12	75	9	0	0	9
	310	10 Either-sex	9	100	6	3	0	9
		15 Antlered	15	80	12	0	0	12
	314	10 Antlered	9	100	8	0	1	9
	316	2 Either-sex	1	100	1	0	0	1
		5 Antlered	4	100	4	0	0	4
	317	5 Antlered	4	75	3	0	0	3

Table 10. Continued.

Year	Hunting District	Number of Permits	Number of Hunters	Percent Success	Sex and age composition[a] Bulls	Cows	Calves	Total Harvest
1984	318	5 Either-sex	5	80	0	3	1	4
		5 Antlered	5	60	3	0	0	3
	322	5 Either-sex	5	80	0	3	1	4
		10 Antlered	8	100	8	0	0	8
	328	3 Antlered	3	67	1	0	1	2
	361	10 Either-sex	9	89	6	2	0	8
		15 Antlered	14	100	10	0	4	14
1985	306	3 Either-sex	3	100	2	1	0	3
		10 Antlered	10	60	6	0	0	6
	307	5 Antlered	5	80	4	0	0	4
		2 Either-sex	2	100	2	0	0	2
	309	5 Either-sex	5	100	3	2	0	5
		15 Antlered	13	85	11	0	0	11
	310	10 Either-sex	8	100	3	3	2	8
		15 Antlered	13	92	10	0	2	12
	314	10 Antlered	10	70	6	0	1	7
	316	2 Either-sex	2	100	1	1	0	2
		5 Antlered	4	75	3	0	0	3
	317	5 Antlered	5	80	4	0	0	4
	318	5 Either-sex	5	60	2	0	2	4
		5 Antlered	4	75	1	1	0	3
	322	5 Either-sex	5	100	2	3	0	5
		10 Antlered	10	70	7	0	0	7
	328	3 Antlered	3	67	1	0	1	2
	361	10 Either-sex	10	100	5	5	0	10
		15 Antlered	15	80	12	0	0	12
1986	306	3 Either-sex	3	100	0	3	0	3
		10 Antlered	10	80	7	1	0	8
	307	4 Antlered	4	75	3	0	0	3
		2 Either-sex	2	100	1	1	0	2
	309	5 Either-sex	5	60	0	3	0	3
		10 Antlered	10	88	8	0	1	9
	310	10 Either-sex	10	100	2	6	2	10
		15 Antlered	15	60	9	0	0	9
	314	10 Antlered	9	33	3	0	0	3
	316	5 Either-sex	5	60	0	3	0	3
		5 Antlered	4	100	4	0	0	4
	317	3 Antlered	3	67	2	0	0	2
		4 Antlerless	3	100	0	3	0	3
	318	5 Either-sex	4	75	0	3	0	3
		5 Antlered	5	60	3	0	0	3
	322	5 Either-sex	5	100	0	5	0	5
		10 Antlered	8	100	8	0	0	8

Table 10. Continued.

Year	Hunting District	Number of Permits	Number of Hunters	Percent Success	Sex and age composition[a]			Total Harvest
					Bulls	Cows	Calves	
1986	328	2 Antlered	2	100	2	0	0	2
	361	10 Either-sex	4	100	4	3	3	10
		15 Antlered	15	100	14	0	1	15

[a] Totals under age and composition do not always equal numbers under total harvest but they are reported as they occurred in the Montana harvest reports.

[b] Includes 1 unclassified moose in the total.

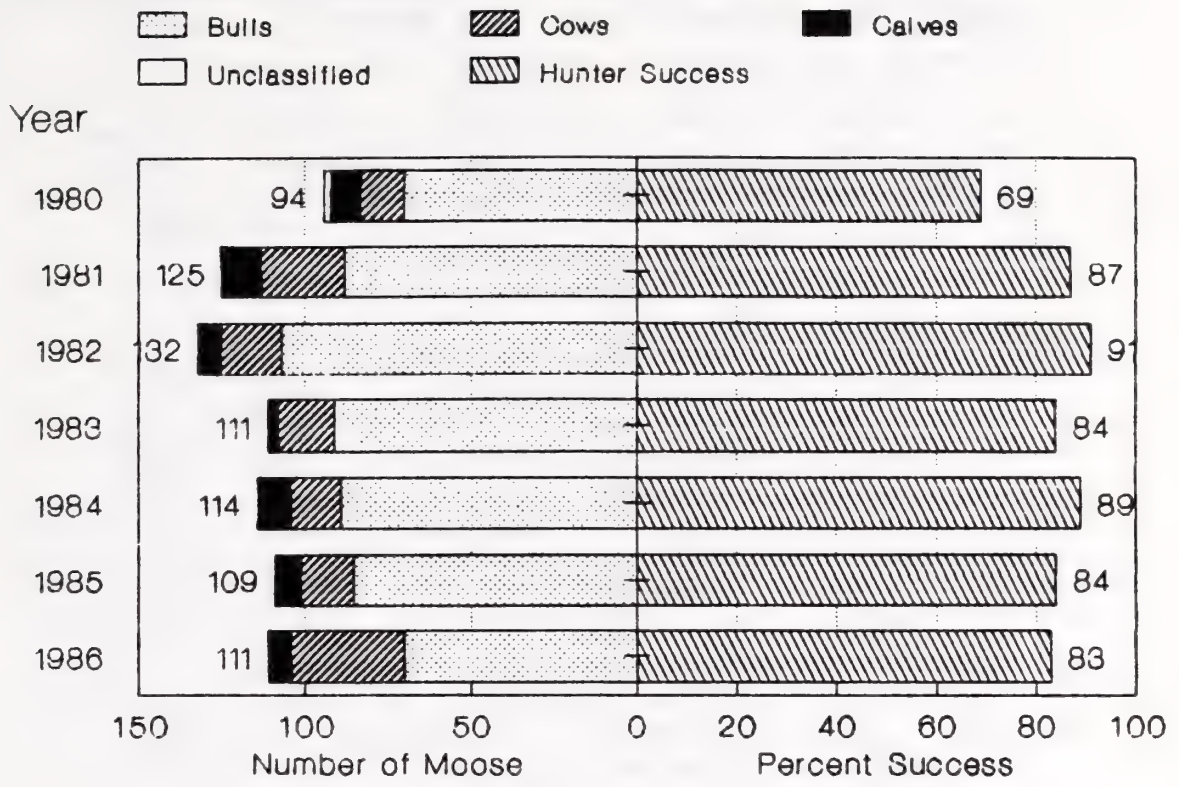


Fig. 14. Total number of moose (bulls, cows, calves and unclassified) harvested and average percent hunter success from 8 Montana areas (11 districts) north of Yellowstone Park, 1980-1986.

Table 11. Montana Dept. of Fish, Wildlife and Parks Region 3 bighorn sheep harvest survey results 1980-1986 (from Alt and Foss 1987, Swenson 1985, Simmons et al. 1984, 1987).

Year	Hunting District	Number of Licenses	Number of Hunters	Harvest[a]	Percent Success
1980	300	126 Unlimited	72	3	4
		5 Limited	5	4	80
	301	136 Unlimited	65	6	9
	302	63 Unlimited	40	1	2
	303	98 Unlimited	65	2	3
		5 Limited	5	5	100
	500	78 Unlimited	35	4	11
	501	89 Unlimited	46	3	7
1981	300	206 Unlimited	134	8	6
		3 Limited	3	3	100
	301	167 Unlimited	122	6	5
	302	140 Unlimited	117	5	4
	303	120 Unlimited	67	1	1.5
		2 Limited	2	1	50
	500	52 Unlimited	42	0	0
	501	93 Unlimited	63	0	0
1982	300	183 Unlimited	117	6	5
	301	138 Unlimited	74	4	5
	302	86 Unlimited	57	3	5
	303	51 Unlimited	18	0	0
	500	50 Unlimited	33	1	3
	501	54 Unlimited	26	2	8
1983	300	181 Unlimited	105	7	7
		3 Limited	3	2	67
	301	94 Unlimited	56	0	0
	302	93 Unlimited	71	3	4
	303	34 Unlimited	13	0	0
	500	88 Unlimited	56	4	7
		2 Limited	2	2	100
	501	75 Unlimited	38	3	8
1984	300	193 Unlimited	76	4	5
		2 Limited	2	2	100
	301	122 Unlimited	65	6	9
	302	60 Unlimited	21	2	9
	303	57 Unlimited	12	0	0
	500	47 Unlimited	26	2	8
		1 Limited	1	1	100
	501	62 Unlimited	44	3	7

Table 11. Continued.

Year	Hunting District	Number of Licenses	Number of Hunters	Harvest[a]	Percent Success
1985	300	84 Unlimited	54	3	6
		2 Limited	2	2	100
	301	106 Unlimited	64	2	3
	302	34 Unlimited	29	0	0
	303	41 Unlimited	17	1	6
	500	52 Unlimited	32	2	6
	501	52 Unlimited	38	2	5
1986	300	102 Unlimited	66	3	5
		2 Limited	2	2	100
	301	207 Unlimited	130	6	5
	302	207 Unlimited	130	6	5
	303	34 Unlimited	14	2	14
		2 Limited	2	1	50
	500	40 Unlimited	21	1	5
	501	99 Unlimited	74	2	3

[a] Harvest consisted of only 3/4 curl rams.

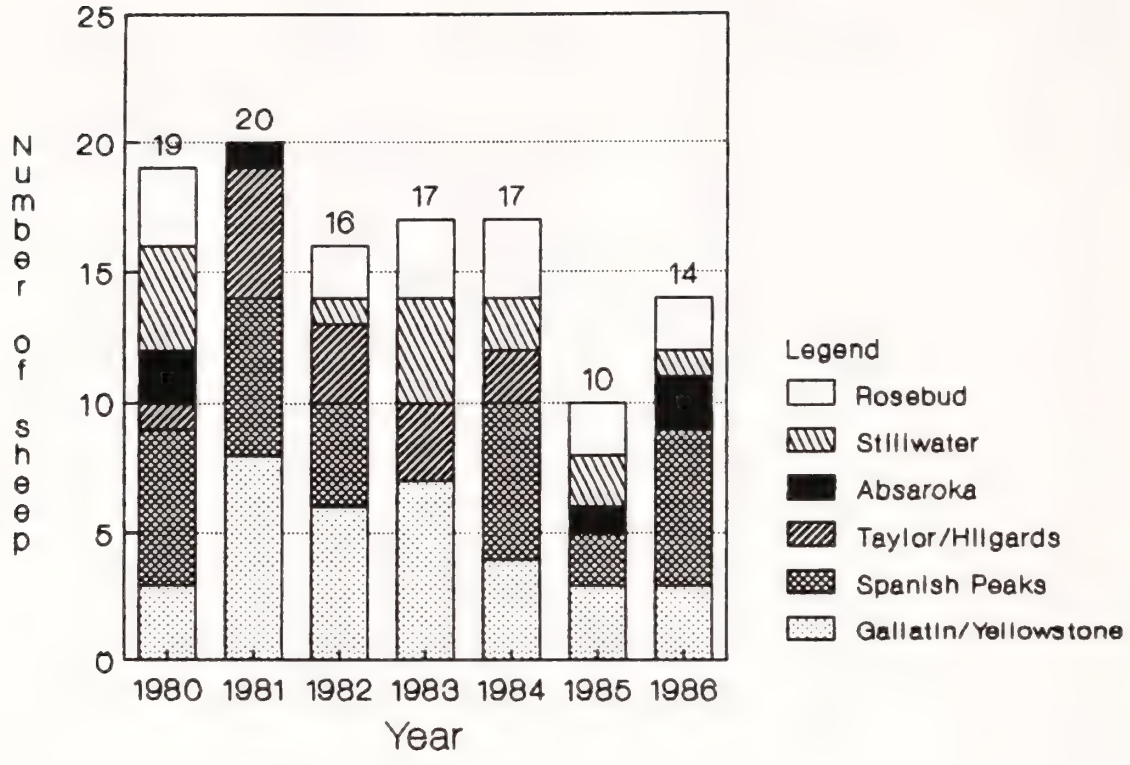


Fig. 15. Number of sheep harvested from 6 Montana hunting areas north of Yellowstone Park, 1980-86. In 1986, the Spanish Peaks and Taylor/Hilgards areas (districts 301 and 302, respectively) had a combined quota applying to both areas. The total harvest from both areas is included only for the Spanish Peak area.

Table 12. Mule deer population trend data (deer classifications) for Montana hunting districts 313 and 314 north of Yellowstone National Park, 1979-1989 (from Foss 1986 and Lemke and Singer 1989).

District	Year	Post Season[a] B/100 D	F/100 D	F/100 A	N	Spring F/100 A	N	Percent Fawn Mort.	Percent Recruitment
313									
	79-80	17	67	52	345	40	91	23	29
	80-81			61	286				
	81-82	15	65	56	97	40	300	29	29
	82-83			55	381	48	727	13	32
	83-84	7	65	60	303	29	420	52	23
	84-85	21	88	73	159	47	508	36	32
	85-86	0	42	42	68	44	562	0	31
	86-87					47	493		
	87-88[b]					45	649		
	88-89[c]					14	1796		
314	79-80			41	62	54	1270	0	35
	80-81					73	339		43
	81-82					45	148		31
	82-83			57	155	52	320	9	34
	83-84	14	73	64	148	40	259	38	29
	84-85	9	59	54	77	46	277	15	31
	85-86	4	43	42	182	34	168	19	26
	86-87					48	295		
	87-88[d]					55	1287		
	88-89[c]					14	1796		

[a] B/100 D = Bucks/100 Does, F/100 D = Fawns/100 Does, F/100 A = Fawns/100 Adults.

[b] Includes helicopter and ground surveys.

[c] Includes portions of districts 313 and 314 (east and west side of the Yellowstone River).

[d] Includes only ground surveys.

Population Trends

Deer

Since 1980 the mule deer population north of Yellowstone National Park has stable or increasing. In response to the increasing populations, Montana Department of Fish, Wildlife, and Parks increased the number of antlerless licenses available to harvest the productive doe population. As early as 1981, concern developed that unpredictable influxes of elk on winter range north of the park made management of deer populations difficult (Foss 1983). Foss (1983) indicated spring fawn/100 adult ratios appeared to be negatively correlated with the number of elk present on the northern winter range. However, Houston (1982) found indices of recruitment for mule deer showed no significant association with elk numbers. Overall, spring fawn recruitment on the east and west sides of the Yellowstone River averaged 29% and 33%, respectively (Table 12).

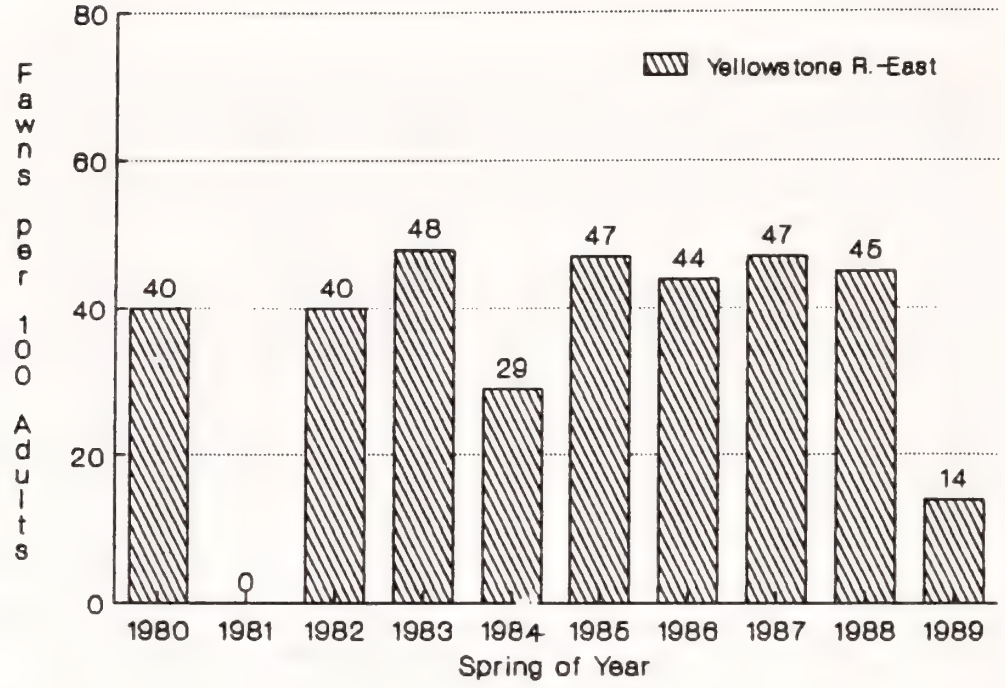
In spring 1981, classification was not done on the east side of the river but indications on the west side suggested high survival. It appears the west side has slightly more fawns/100 adults than the east but trends for both are similar. Since 1980 fawn survival was relatively stable (even with increasing female harvest) owing to the relatively mild winters, especially since 1984 (Fig. 16). The harsh winter of 1983-1984 contributed to a large drop in the spring fawn/100 adult ratio. This rebounded and remained relatively stable until 1988-1989. The combination of the drought in 1988, deep snows and cold temperatures in early 1989 contributed to significant winter loss of deer (Lemke and Singer 1989, Singer et al. 1989) and may explain the low fawn/adult ratio for 1989. Trend data for other districts surrounding the park were not collected.

Moose

Aerial classification data are not collected for moose populations in Montana hunting districts surrounding Yellowstone National Park. This is partly due to moose remaining in the timber and their subsequent low observability. However, hunter reported observations of moose can yield trends in the moose population. The data from Hellroaring, Buffalo Fork, Slough Creek, and Upper Stillwater (districts 316, 317, 318, and 322, respectively) in the Absaroka high country have suggested an increasing moose population since initiating more restrictive permit regulations in the mid-1970s (Table 13). Number of moose seen per hunter significantly increased during the period of 1979-1986 compared to 1975-1978 (Swenson 1984b, 1986; Swenson and Foss 1986). This coupled with a lower reported calf/100 cows ratio (Fig. 17), suggesting reduced quality and/or quantity of forage (Schladweiler 1974), was the justification for Montana to issue more antlerless only permits in this area. No population trend data for districts bordering the northwest corner of the park are collected annually.

Table 13. Number of moose seen per hunter and the number of calves per 100 cows reported by hunters for selected Montana hunting areas surrounding Yellowstone National Park, 1975-1985. (Adapted from Swenson and Foss 1986).

	Hunting area									
	Upper Yellowstone		Hellroaring		Buffalo Fork		Slough Creek		Upper Stillwater	
Year	Moose/ Hunter	Calves/ 100 Cows	Moose/ Hunter	Calves/ 100 Cows	Moose/ Hunter	Calves/ 100 Cows	Moose/ Hunter	Calves/ 100 Cows	Moose/ Hunter	Calves/ 100 Cows
1975	1.9	52	2.7	12	5.5	18	5.7	44	4.8	50
1976	2.0	60	7.5	38	5.4	19	1.8	25	3.2	57
1977	1.5	33	3.6	11	1.3	0	4.3	29	2.0	25
1978	3.0	44	3.0	23	3.0	100	3.7	57	2.1	33
1979	2.1	58	2.4	50	16.0	21	3.3	38	4.7	27
1980	1.7	53	4.4	29	3.0	50	7.5	24	2.9	18
1981	3.9	40	4.8	0	6.8	0	5.0	57	4.6	50
1982	5.4	33	4.8	0	12.2	45	8.2	0	8.4	27
1983	6.8	22	6.0	20	3.5	100	5.3	38	6.7	4
1984	6.8	50	6.7	0	19.0	0	7.3	50	8.3	18
1985	6.0	38	5.8	11	6.6	7	4.5	71	5.0	82



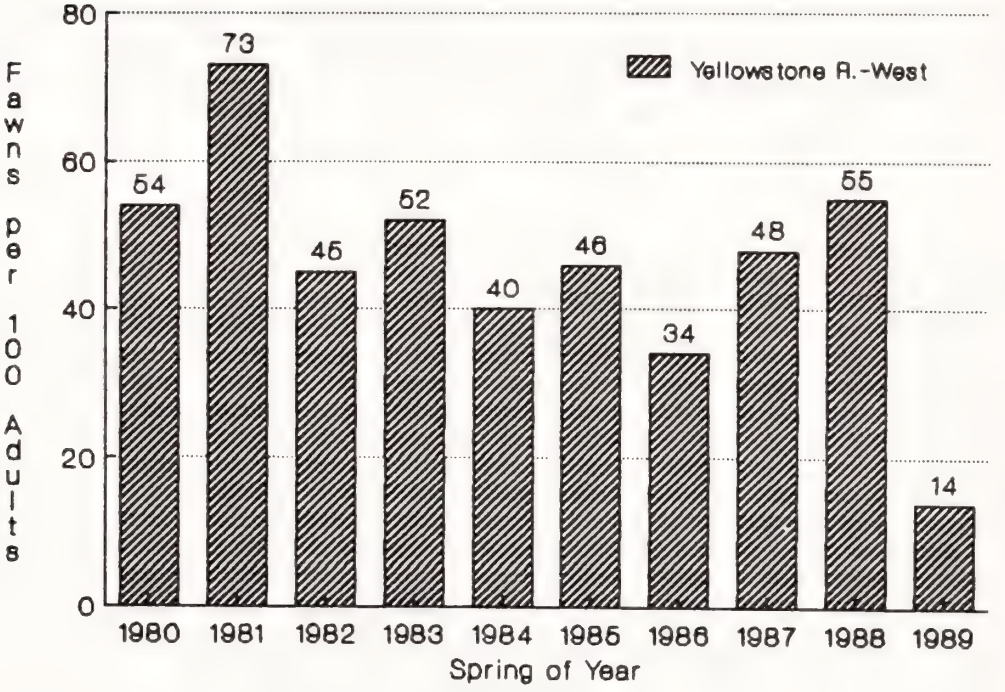


Fig. 16. Fawns/100 adults calculated from spring deer classifications for Yellowstone River-East (district 313) and Yellowstone River-West (314) areas in Montana north of Yellowstone Park, 1980-1989.

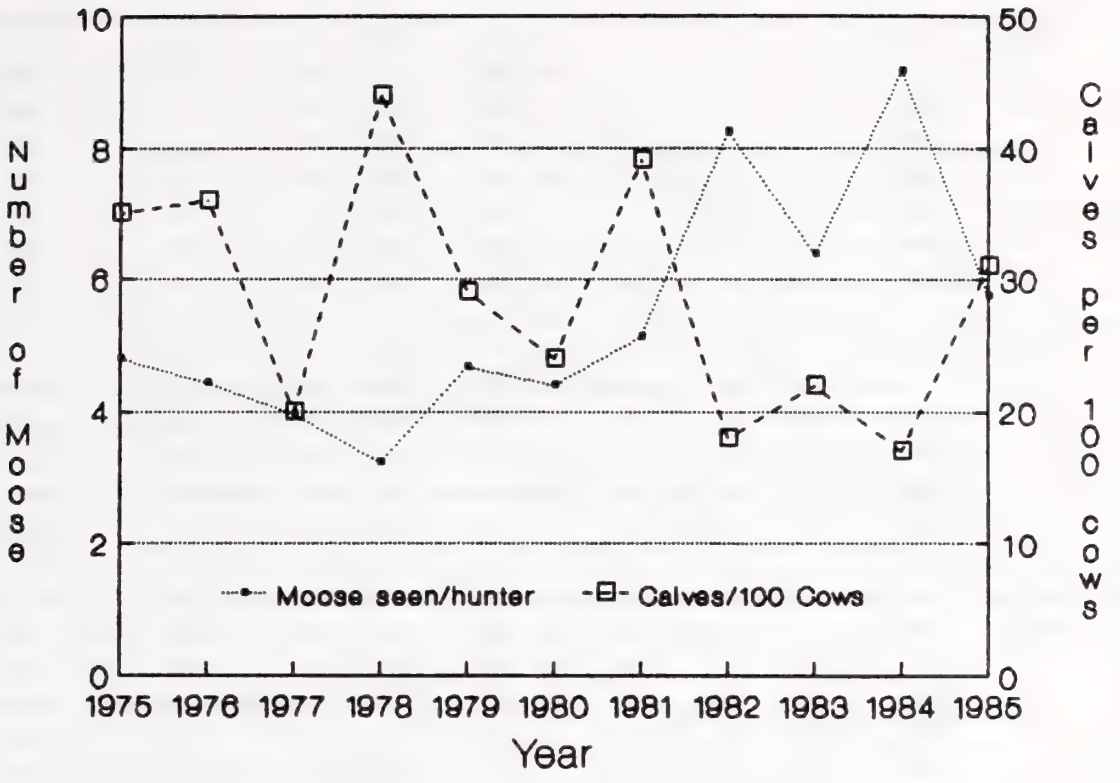


Fig. 17. Calves/100 cows and moose seen/hunter as reported by moose hunters hunting in the Hellroaring (district 316), Buffalo Fork (317), Slough Creek (318), and Upper Stillwater (322) areas of Montana north of Yellowstone Park, 1975-85.

Table 14. Bighorn sheep population classification data for hunting districts adjacent to Yellowstone Park in Regions 3 and 5 of Montana, 1980-1986.

Year	Hunting District	RAMS 0-1/4	1/4-1/2	1/2-3/4	3/4+	Total	Ewes	Lambs	Unclassified	Total Classified	Lambs/ 100 ewes	Rams/ 100 ewes
1980-81	300 TM[a]	0	0	5	10	15	33	22	17	70	67	45
	C[b]	2	3	7	10	22	45	18	0	85	40	49
	301	6	7	9	5	27	55	34	5	116	62	51
	302[c]	3	4	4	8	19	29	11	31	59	38	70
	303[d]	8	8	12	40	68	100	45	4	213	45	68
	303[e]	2	2	5	7	16	27	5	0	48	18	59
	500	-	-	-	-	14	27	11	0	52	46	54
	501[f]	-	-	-	-	13	28	9	0	24	64	46
1981-82	300 TM	7	5	2	8	22	29	15	2	66	51	76
	C	5	4	3	17	29	49	17	0	95	35	59
	301	7	5	7	0	19	38	14	9	71	37	50
	302	8	3	3	2	16	26	10	0	52	38	62
	303[d]	11	3	5	23	42	74	33	7	149	45	55
	500	-	-	-	-	18	26	11	0	55	46	54
	501	-	-	-	-	6	11	7	0	44	52	55
1982-83	300 TM	1	2	5	4	12	26	10	45	48	38	46
	C	11	6	4	20	41	68	22	0	131	32	60
	301	6	6	5	3	20	76	14	0	110	18	26
	302[g]	0	0	2	9	11	17	4	25	32	24	65
	303[h]	8	15	6	7	36	26	7	3	69	27	138
	500	-	-	-	-	16	20	6	0	42	33	77
	501	-	-	-	-	12	21	11	0	69	31	47
1983-84	300 TM	2	1	6	2	11	24	12	43	47	50	46
	C	7	11	5	12	35	63	8	0	106	13	56
	301 302[i]	7	5	17	1	30	73	43	0	146	59	41
	303[j]	4	9	5	3	21	15	2	0	38	13	140
	500	-	-	-	-	23	19	6	0	48	33	78
	501	-	-	-	-	22	36	11	0	56	33	61
1984-85	300 TM	3	0	6	8	27[k]	25	6	27	58	24	60[l]
	C	2	6	6	10	24	44	11	0	79	25	55
	301 302[i]	2	4	4	3	13	35	21	0	69	60	37
	303	2	2	8	9	21	19	6	0	46	32	110
	500	-	-	-	-	10	19	5	0	34	28	50
	501	-	-	-	-	20	27	9	0	34	33	74
1985-86	300 TM	-	-	5	8	13	26	7	8	46	27	50
	C	5	2	2	14	23	48	21	0	92	44	48
	301[i] 302[i]											
	303	4	3	5	13	25	24	10	0	59	42	104
	500	-	-	-	-	10	28	6	0	100	33	27
	501	-	-	-	-	17	10	3	0	34	33	210

Table 14. Continued.

Year	Hunting District	RAMS 0-1/4	1/4-1/2	1/2-3/4	3/4+	Total	Ewes	Lambs	Unclassified	Total Classified	Lambs/ 100 ewes	Rams/ 100 ewes
1986-87	300 TM	1	1	1	8	11	23	6	0	40	26	48
	C	6	6	3	6	21	41	16	0	78	39	51
	301[i]											
	302[i]											
	303	1	1	5	10	17	12	4	0	33	33	142
	500	-	-	-	-	11	18	11	0	40	73	60
	501[i]											

[a] TM= Tom Miner population; the maximum count for each category was used from a series of visits. This applies to all years hereafter.

[b] C=Cinnabar population; the maximum count for each category was used from a series of visits. This applies to all years hereafter.

[c] Dates ranged from 29 October 1980 to 1 May 1981, and the maximum count for each category was used from a series of visits. Primary data used are from 8, 13, and 27 January 1981.

[d] Sheep classified in Yellowstone Park.

[e] Sheep classified elsewhere within the district.

[f] Hunting District 501 classifications were done in spring.

[g] Dates ranged from 10 December 1982 to 6 April 1983, and the maximum count for each category was used from a series of visits.

[h] A portion of classified animals are from Yellowstone Park.

[i] No classifications were done for this district.

[j] Maximum totals for eack category in the south portion of the district (also includes animals in Yellowstone Park). This applies to all years hereafter.

[k] Includes ten unclassified rams.

[l] Calculated from lamb/ewe ratio assuming that 20 of 25 unclassified "ewes and lambs" were ewes and added these to the ewe count for this ratio.

Bighorn Sheep

Bighorns inhabit three winter ranges in and adjacent to Yellowstone National Park. These winter ranges (Fig.18) include the Mount Everts-Specimen Ridge, Cinnabar Mountain, and Tom Miner Basin (Keating 1982, 1985; Irby et al. 1986; Meagher, Natl. Park Serv., pers. comm.). The majority of bighorns in the Mount Everts-Specimen Ridge population reside in Yellowstone National Park. Bighorn sheep in the Cinnabar Mountain population winter outside Yellowstone, but summer inside the park on Sepulcher Mountain, Electric Peak, Bannock Peak, and Quadrant Mountain (Fig. 18). Bighorns from the Tom Miner Basin population winter outside the park. Summer ranges for this population straddle the park boundary on Sheep Mountain, Ramshorn Peak, and Fortress Mountain (Keating 1982). Population trends and subsequent bighorn sheep management north of Yellowstone is related to numbers of bighorns classified on winter ranges (Table 14) and lamb/100 ewes ratios.

The Mount Everts-Specimen Ridge population is larger than the Cinnabar Mountain or Tom Miner populations. Bighorns on Mount Everts (excluding the Specimen Ridge area) increased from 63 in 1965 to a maximum of 222 in 1978. The rapid rate of increase from 1965 to 1973 was estimated to be 12% per year (Keating 1982).

This bighorn sheep population was relatively stable from 1974 to 1981 and numbered about 200 (Keating 1982). M. Meagher (pers. comm.) estimated the Mount Everts-Specimen Ridge population to be about 400 animals, but an infectious keratoconjunctivitis epidemic in 1982 reduced the population 75%-85% (Meagher 1982; M. Meagher, Natl. Park Serv., pers. comm.; Fig. 19). The Mount Everts-Specimen Ridge population has recovered to a minimum of 136 individuals (M. Meagher, pers. comm.).

Bighorns were extirpated from the Cinnabar Mountain population (hunting district 300) in the late 1800s. Following recolonization from Mount Everts in 1965, the herd rapidly grew from 11 in 1967 to 103 in 1980 (18% per year) (Keating 1982). This population has continued to grow. Irby et al. (1986) estimated 80-150 bighorns occupy the Cinnabar Mountain winter range. Lamb/ewe ratios have been negatively correlated to the number of ewes present in a population the previous year (Fig. 20) and indicate too many bighorns for the forage conditions (Swenson 1985). The growing population and low lamb/ewe ratios led the Montana Department of Fish, Wildlife and Parks to transplant 13 individuals from the Cinnabar herd to Mill Creek in the Absaroka area (district 303) in 1985.

The Taylor/Hilgards area (district 302) probably never had many bighorns in the last ten years. This area is probably inconsequential to wolf recovery because of the distance of the bighorn sheep herds from Yellowstone National Park. This district contains three small bands of bighorns and the most numerous band (Hilgards area) experienced a drastic decline in numbers (Swenson 1985). This decline probably resulted from competition with increasing numbers of elk on winter range and possibly an increase in the mountain goat population in this area (Swenson 1985).

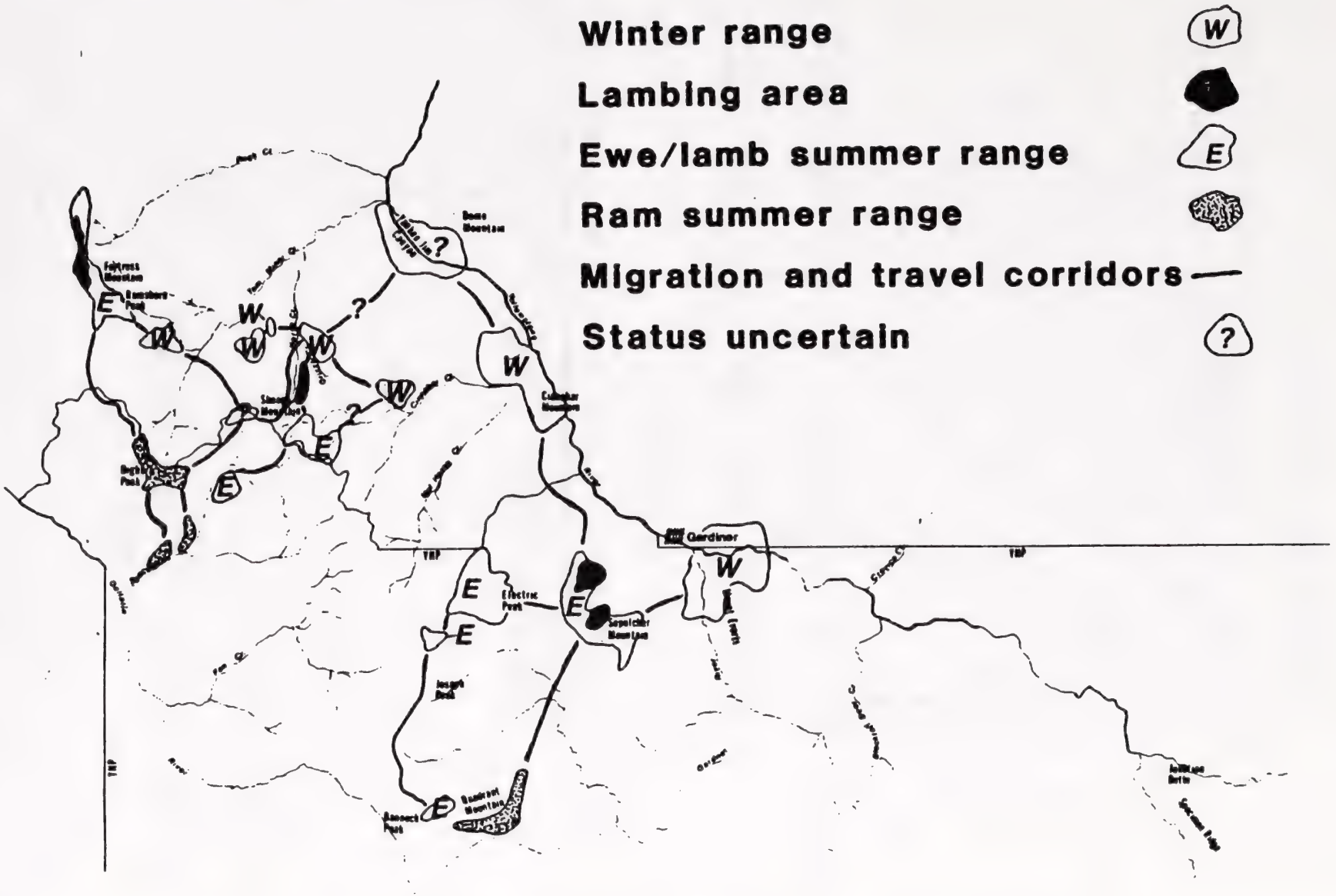


Fig. 18. Map of winter ranges for the Mount Everts, Cinnabar Mountain, and Tom Miner Basin bighorn sheep populations (Keating 1982).

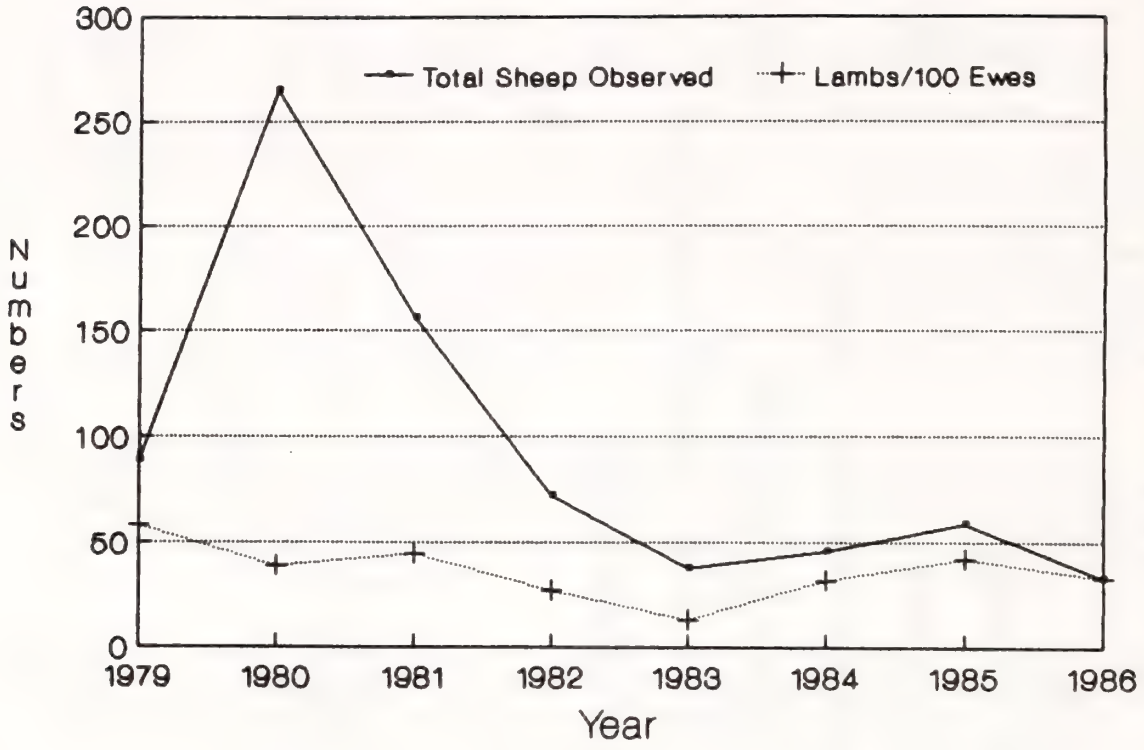
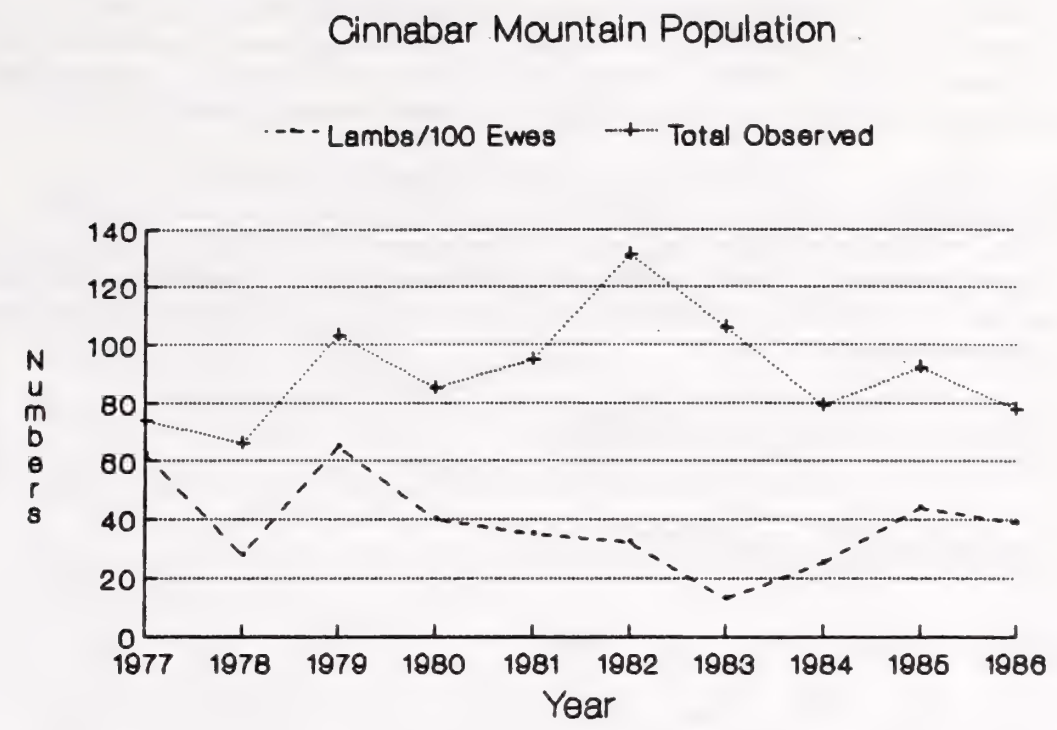


Fig. 19. Lambs/100 ewes and total number of bighorn sheep observed during classifications conducted in north-central Yellowstone Park and the Absaroka (district 303) hunting area of Montana adjacent to the Park, 1979-86.



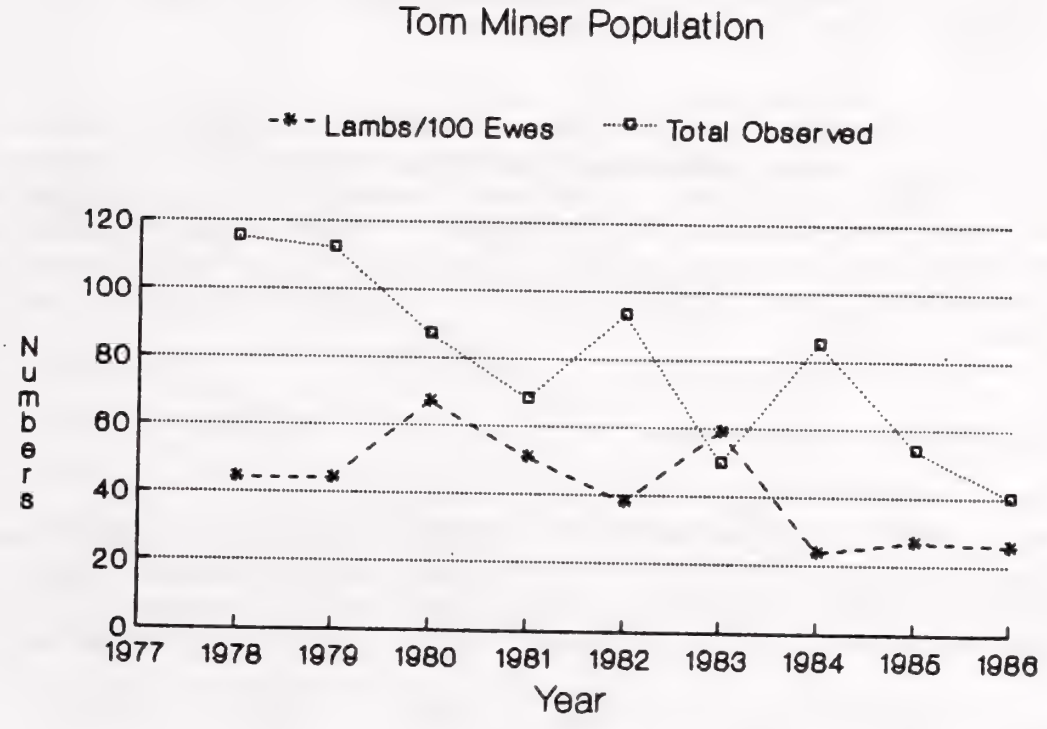


Fig. 20. Lambs/100 ewes and total number of bighorn sheep observed during classifications of the Cinnabar Mountain and Tom Miner populations in the Gallatin/Yellowstone (district 300) hunting area in Montana north of Yellowstone Park, 1977-86.

The bighorn sheep population in the Stillwater herd (district 500) has declined since the mid-1980s (Fig. 21). Low lamb/100 ewes ratios (except 1987) appear related to increased human activity (mining) near preferred winter range (Simmons et al. 1984). Because of low recruitment, significant increases in the population are not possible (Simmons et al. 1987).

The Rosebud population appeared to be slowly increasing from 1980 to 1987 (Fig. 21). Minimum population counts (numbers classified) were inaccurate for many years because of poor survey conditions. This explains the unusually low number of observed individuals (except for 1983 and 1986 when adequate counts were obtained).

WYOMING DISTRICT II SUMMARIES

Seasonal Ranges and Distribution

Elk

During the spring, elk from the Clarks Fork, North Fork Shoshone, and Carter Mountain herds migrate west from winter ranges into Yellowstone National Park (Figs. 2 and 22). Based upon radiotelemetry studies (Yorgason et al. 1981, Rudd 1982, Rudd et. al. 1983), about 80% of the Clarks Fork and North Fork Shoshone herds migrate into the park.

A small portion of the Carter Mountain herd apparently summers in the Thorofare /Upper Yellowstone River area of the Yellowstone National Park (Fig. 22). Small groups have twice been tracked in the snow from the Thorofare River to South Fork Shoshone winter ranges (in the Carter Mountain herd unit) after crossing the Absaroka Divide in the vicinity of Thorofare Buttes (G. Roby, Wyoming Dept. Game and Fish and F. J. Singer Yellowstone Natl. Park, pers. comm.)

Mule Deer

Mule deer winter east of Yellowstone National Park in the Clarks Fork, North Fork Shoshone, and South Fork Shoshone river drainages (Fig. 23). No radiotelemetry studies have been conducted to determine if Yellowstone provides spring, summer, and fall ranges for any of the three deer herds.

Moose

Moose winter in the Crandall, Sunlight Basin, North Fork Shoshone, and Thorofare areas adjacent to Yellowstone National Park (Fig. 24). Moose from the other three ranges may migrate to summer range in Yellowstone National Park, however, no radiotelemetry studies investigating seasonal ranges have been conducted on these moose populations.

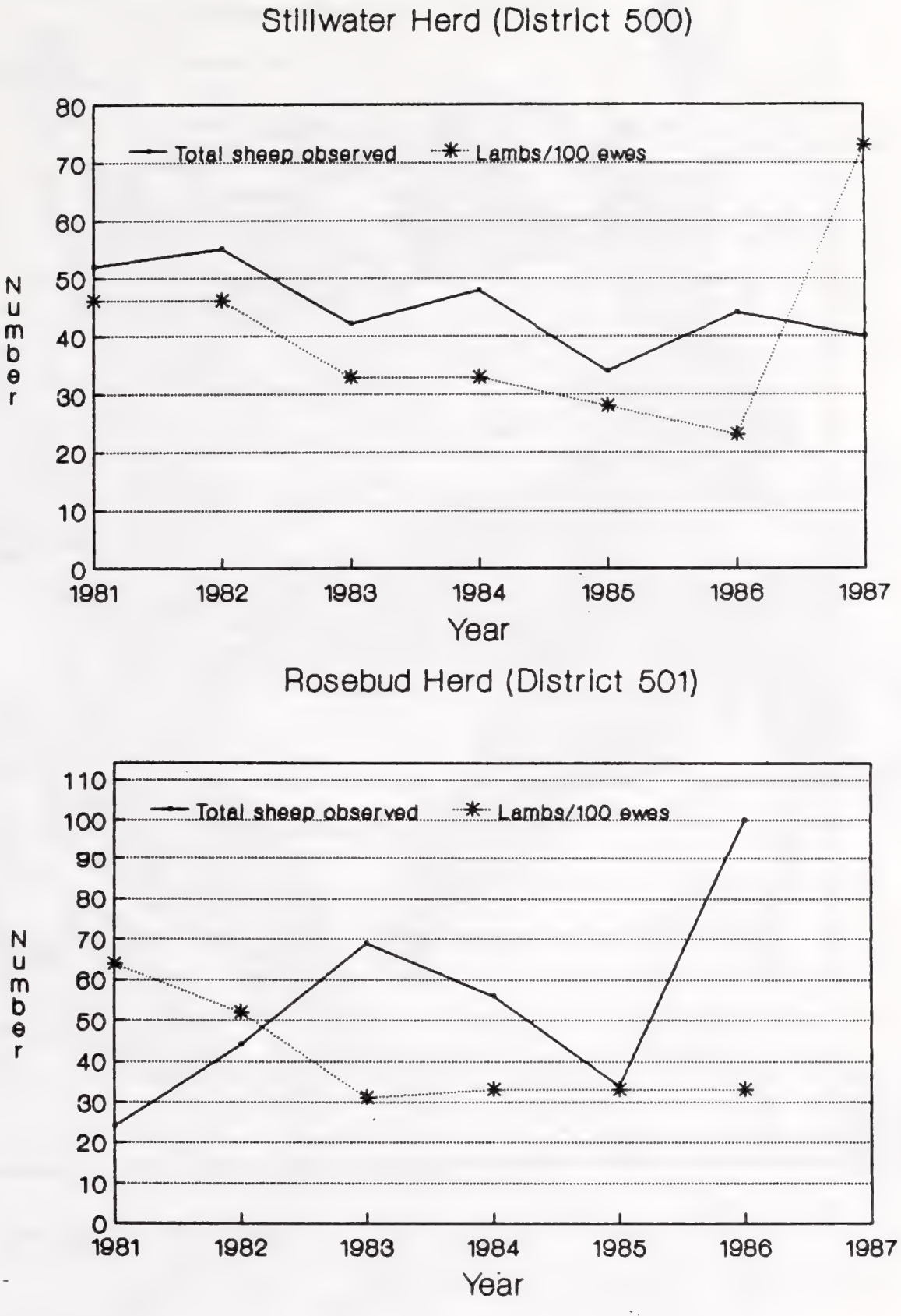


Fig. 21. Lambs/100 ewes and total number of bighorn sheep observed during classifications done in 2 Montana hunting areas adjacent to the northeast corner of Yellowstone Park, 1981-87.

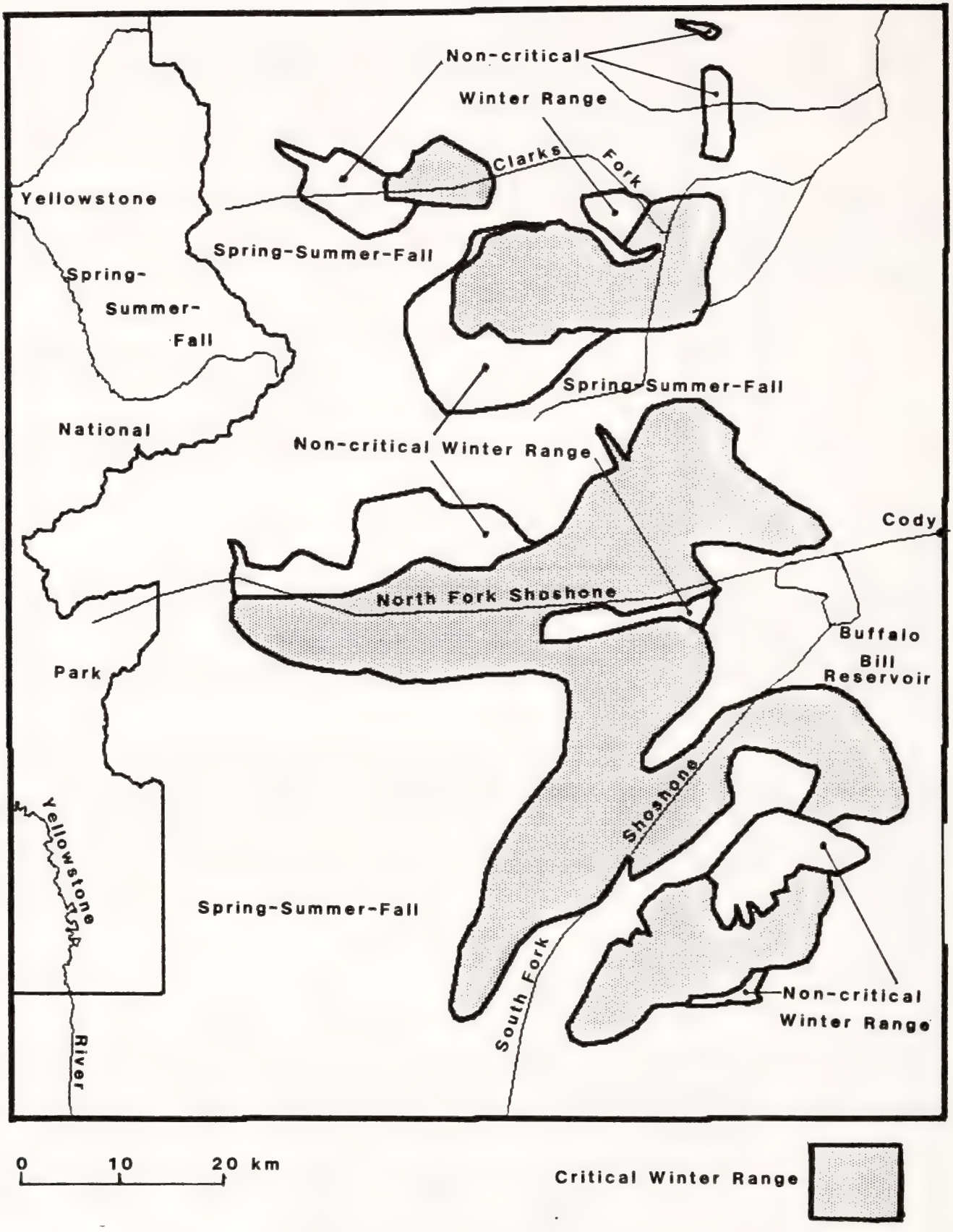


Fig. 22. Spring-summer-fall, and winter ranges for the Clarks Fork North Fork Shoshone, and Carter Mountain elk herds in District II in Wyoming east of Yellowstone Park. Seasonal ranges adapted from Hurley et al. (1989).

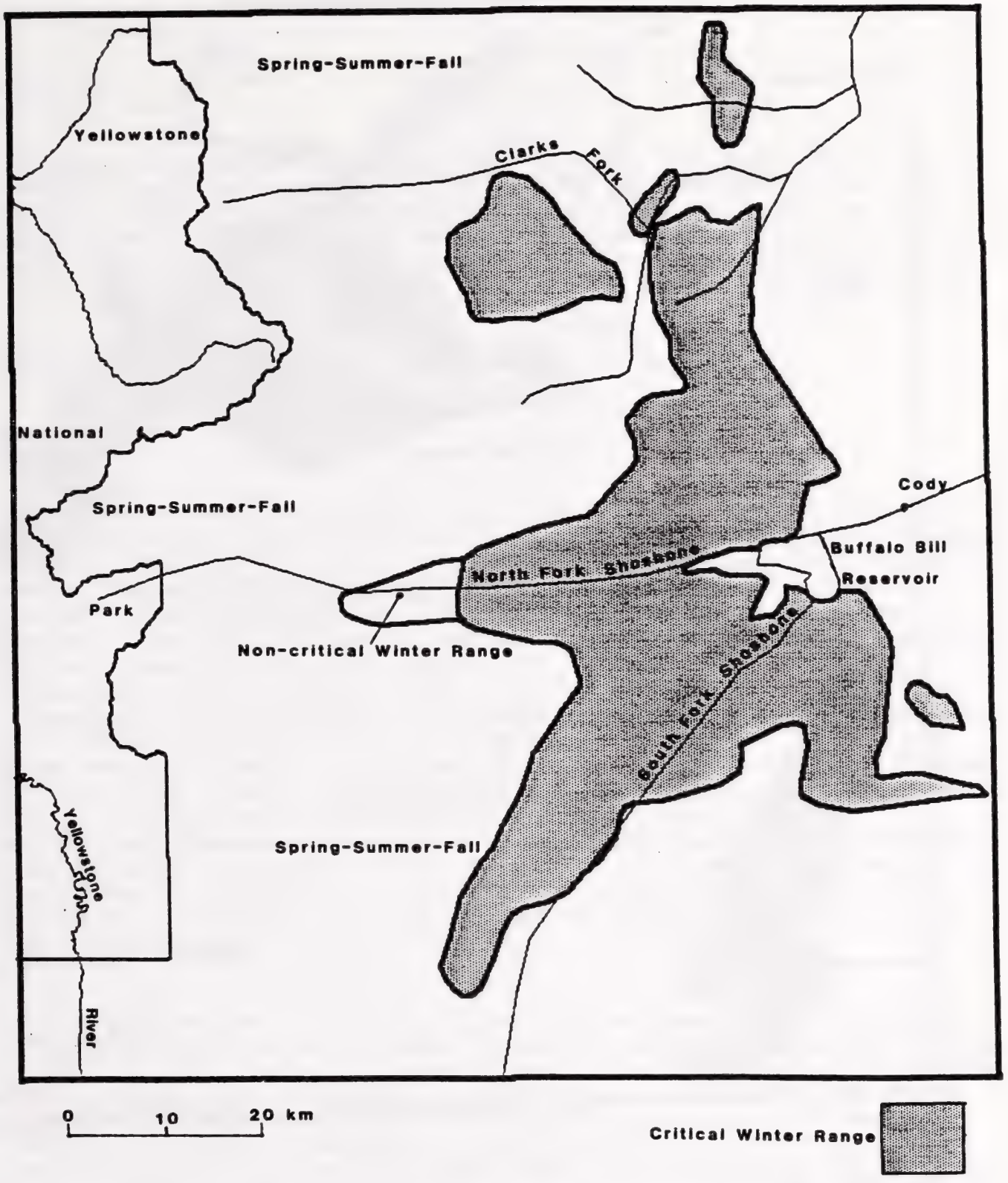


Fig. 23. Spring-summer-fall, and winter ranges for the Clarks Fork, North Fork Shoshone, and South Fork Shoshone mule deer herds in District II in Wyoming east of Yellowstone Park. Seasonal ranges adapted from Hurley et al. (1989).

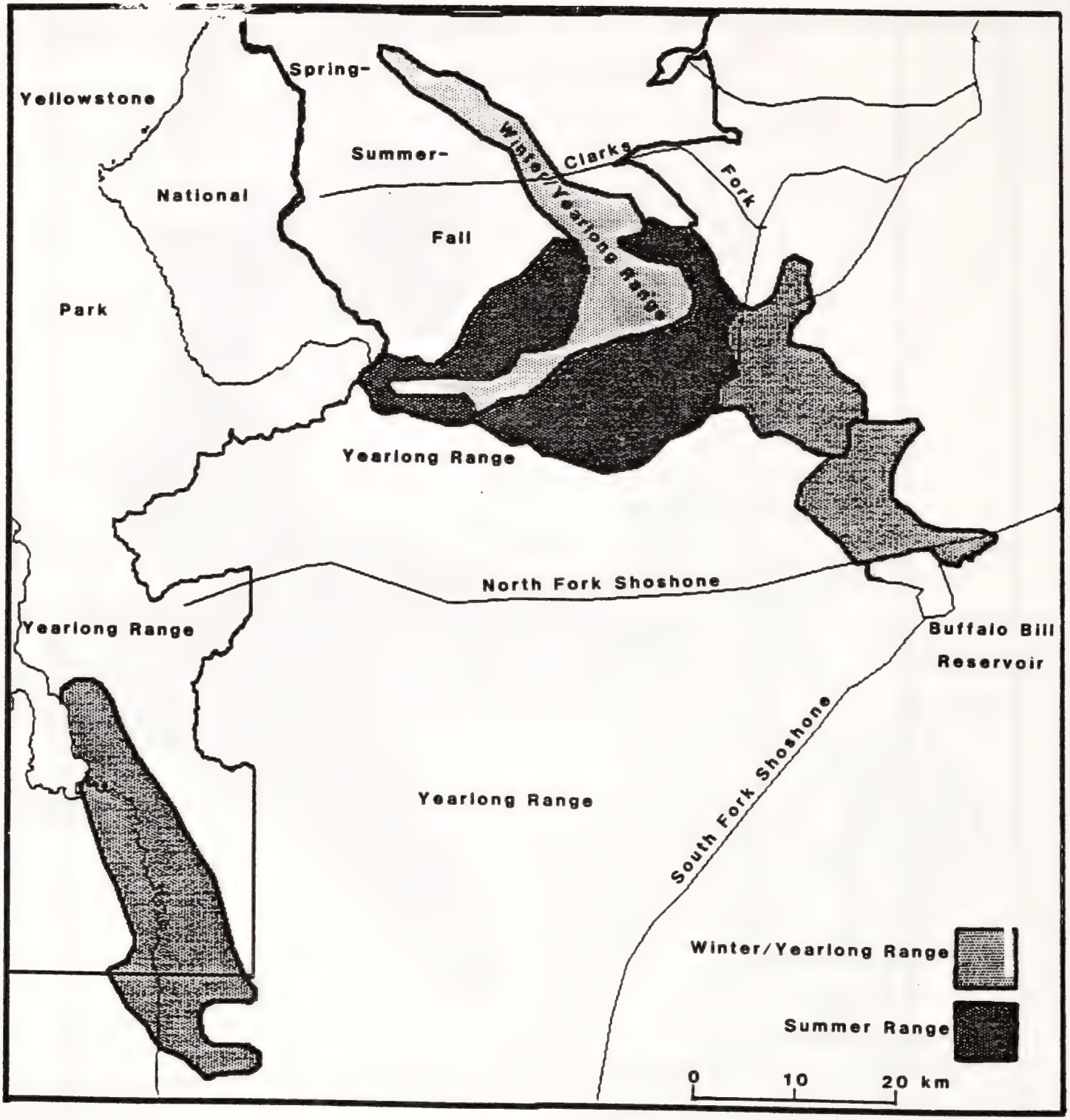


Fig. 24. Spring-summer-fall, and winter ranges for the Crandall, Sunlight, North Fork Shoshone, South Fork Shoshone, and Thorofare moose herds in District II in Wyoming east of Yellowstone Park. Seasonal ranges adapted from Hurley et al. (1989).

Bighorn Sheep

Bighorns in the Clarks Fork, Trout Peak, and Younts Peak areas (Fig.25) primarily reside year-round outside Yellowstone National Park (Hurley 1985, Hurley et al. 1989). However, all three sheep ranges are 8 km-24 km (5-15 miles) from the park and within range of some potential wolf activity. The Wapiti Ridge population occupies summer and winter ranges in the southeastern corner of Yellowstone National Park (Hurley 1985, Hurley et al. 1989, Fig. 25).

Hunting Season Regulations

Elk

Five hunting areas (50-54) comprise the Clarks Fork herd unit, four hunting areas (55-57, 60N) comprise the North Fork Shoshone herd unit, and four hunting areas (58, 59, 60S, and 61) comprise the Carter Mountain herd unit (Fig. 26). Archery seasons for elk progressed from a two week season with no special permits in 1980 to a longer one month season with antlered bull special permits. In Wyoming, the archery seasons occur earlier than rifle seasons and follow the same season restrictions as rifle seasons. From 1980 to 1982, archery seasons for the Clarks Fork, North Fork Shoshone and Carter Mountain (formerly called South Fork Shoshone) herds were approximately two weeks long, opening and closing dates 16 and 30 September, respectively. During these three years, the Clarks Fork also had an earlier season lasting from 26 August to 9 September. Interestingly, the North Fork Shoshone did not have an archery season in 1982. From 1983 to 1989, archery seasons were lengthened approximately two weeks for all three herds. Opening and closing dates were 1 and 30 September, respectively. From 1983 to 1987, some hunting areas had shorter seasons lasting from approximately 26 August to 9 September. In 1988-1989, only people holding special permits could legally hunt during the August opening dates.

Rifle hunting seasons for District II have evolved from long split seasons (1.5 months total) and special either-sex permits (Fig. 27) to shorter seasons (1 month, no split season) with special permits for harvest of antlerless (Fig. 28) or antlered (Fig. 29) animals on specific days. Since 1980, harvest of branch-antlered bulls was limited to the beginning of the general season. Spikes could be legally harvested during the second half of the split season when split seasons were in effect (1980-1985). Due to hunter's concerns about the apparent lack of branch-antlered bulls in the herds, the Wyoming Game and Fish discontinued general season spike harvests coincident with the absence of split seasons in 1986.

Fig. 25. Spring-summer-fall, and winter ranges for the Clark's Fork, Trout Peak, Wapiti Ridge, and Yount's Peak bighorn sheep herds in District II in Wyoming east of Yellowstone Park. Seasonal ranges adapted from Hurley et al. (1989).

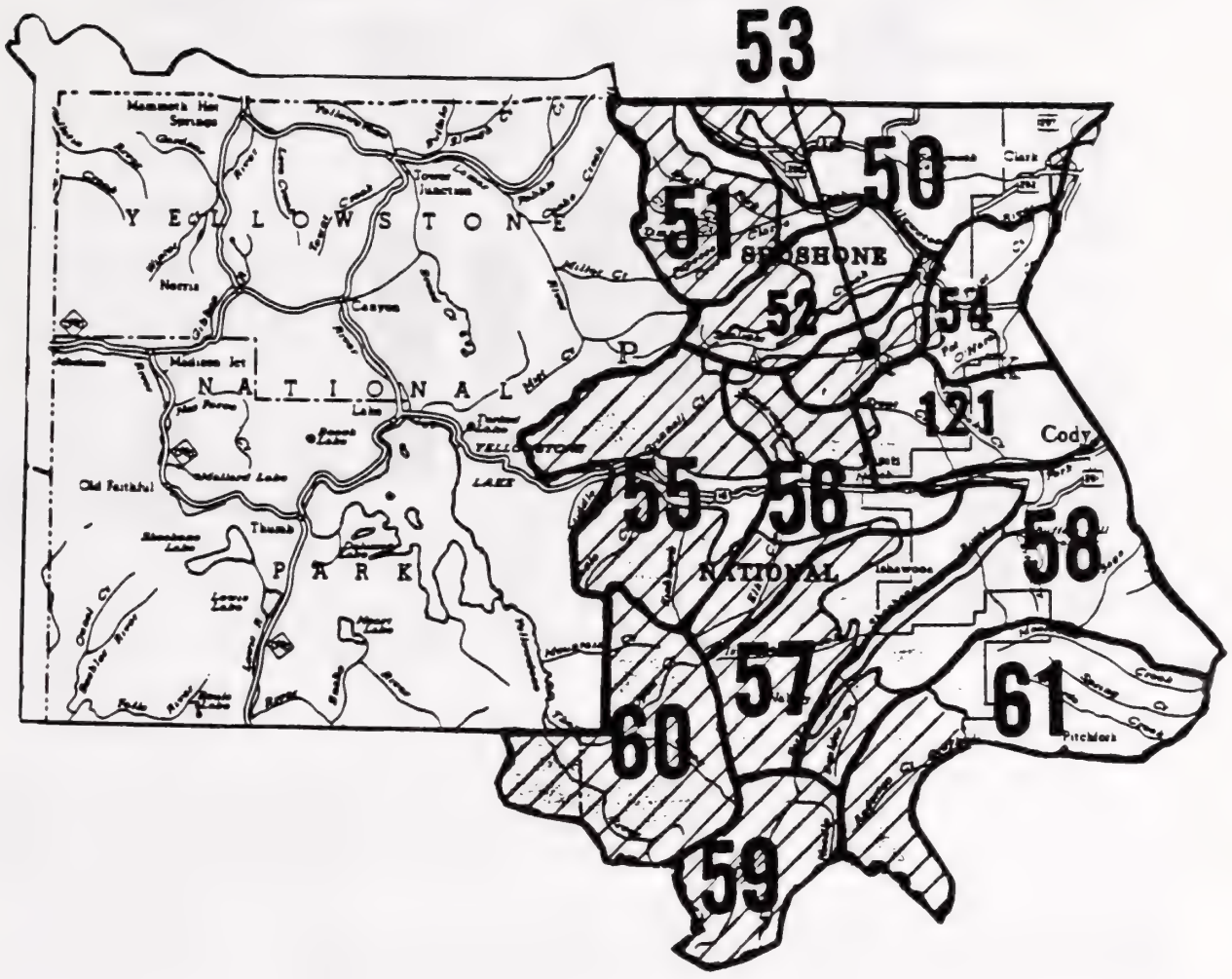


Fig. 26. Hunting area boundaries in District II, Wyoming for the Clarks Fork (hunting areas 50-54), North Fork Shoshone (hunting areas 55-57, 60N), and Carter Mountain (hunting areas 58, 59, 60S, 61) elk herd units east of Yellowstone National Park.

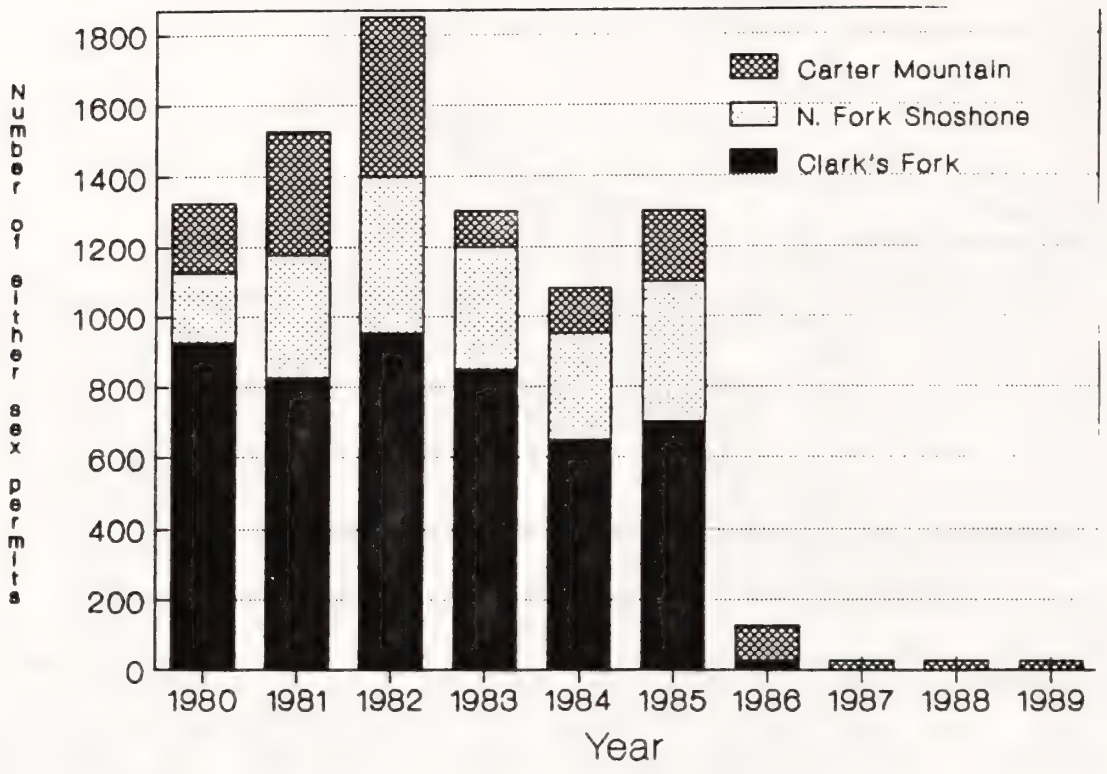


Fig. 27. Number of either-sex special permits offered for the Clarks Fork, North Fork Shoshone, and Carter Mountain elk herd units in Wyoming east of Yellowstone National Park 1980-1988.

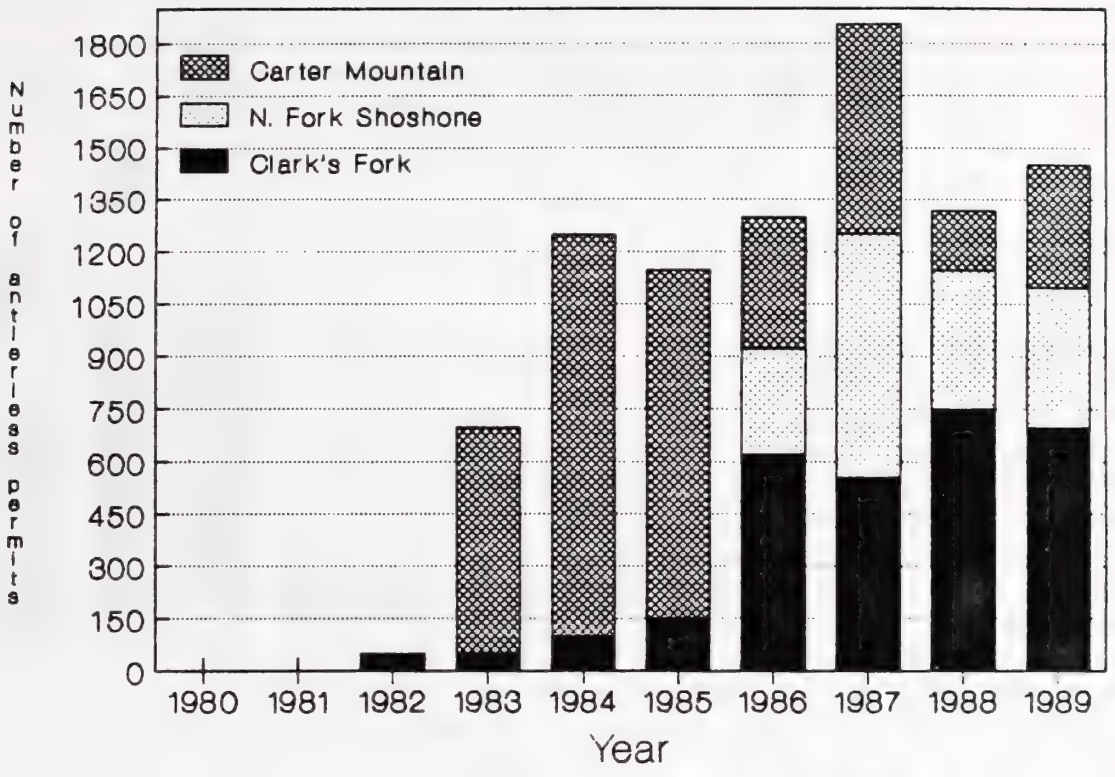


Fig. 28. Number of antlerless special permits offered for the Clarks Fork, North Fork Shoshone, and Carter Mountain elk herd units in Wyoming east of Yellowstone National Park, 1980-1988.

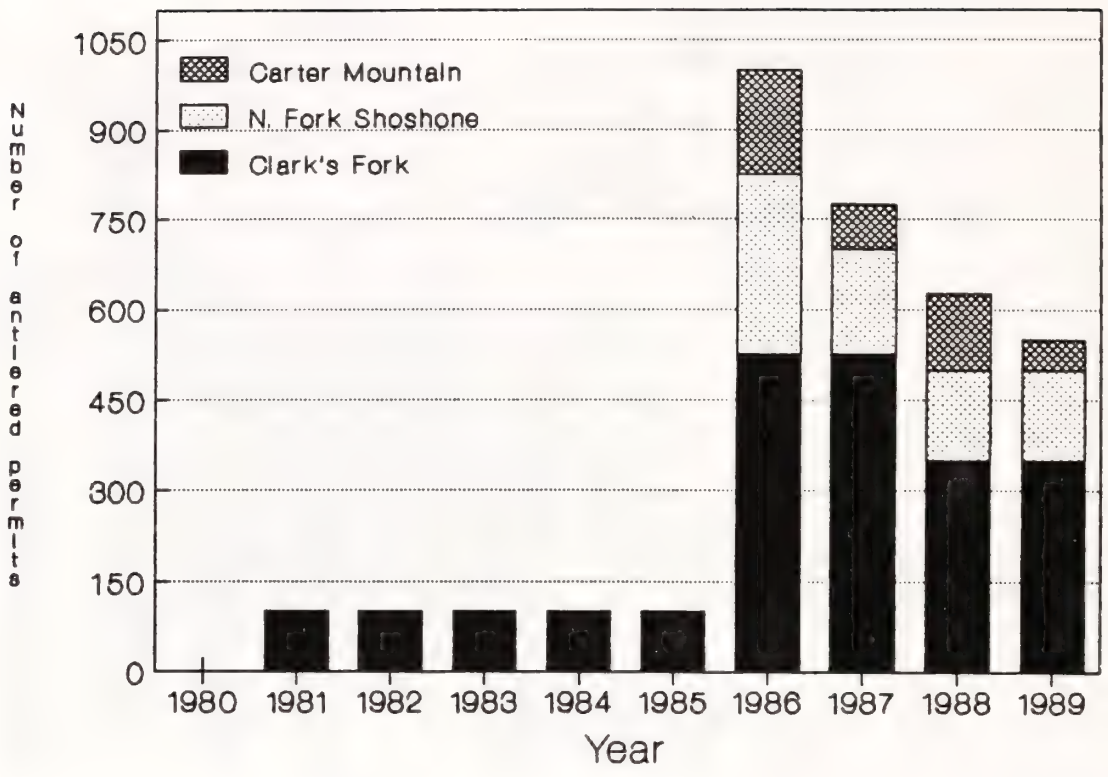


Fig. 29. Number of antlered special permits offered for the Clarks Fork, North Fork Shoshone, and Carter Mountain elk herd units in Wyoming east of Yellowstone National Park, 1980-1988.

In 1980, split seasons were present in all hunting areas of the Clarks Fork, North Fork Shoshone, and Carter Mountain herds. Early seasons lasted from 25 September to 25 October for the Clarks Fork herd and from 1 to 25 October for the North Fork Shoshone and Carter Mountain herds. The second half of the split season generally lasted from the first to the third week in November for all three herds. In 1986, the general season began on 1 October and ended 31 October. This type of general season has remained through 1989. With the end of the split season, hunting opportunities later in the year (November and December) were controlled with special permits.

Special permits

In 1980 and 1981, only either-sex permits were offered for the Clarks Fork, North Fork Shoshone, and Carter Mountain herds. Beginning in 1982, either-sex permits were increased and antlerless only permits appeared (50 in the Clarks Fork herd, Fig. 28). Between 1980 and 1987 the Wyoming Game and Fish Department also issued 100 antlered bull permits for an early season rifle hunt from 10 to 30 September in the Clarks Fork herd. The dramatic increase in antlered permits coincided with the onset of branch-antlered bull seasons (Fig. 29). The sharp increase in the availability of antlerless only permits began in 1983 and coincided with the virtual disappearance of either-sex permits (Fig. 27). In 1980, the total number of either-sex and antlerless only permits was 1,325 and 0, respectively, for the three herds. In 1989, the emphasis on antlerless permits was reflected in the number of either-sex and antlerless permits offered (25 and 1,450, respectively). This change reflects the Wyoming Game and Fish Department's attempt to reduce hunting pressure on bulls and maintain adequate harvests of growing elk populations.

Mule Deer

Five mule deer hunting areas (105-109) comprise the Clarks Fork herd unit, three hunting areas (110, 111, 115N) comprise the North Fork Shoshone herd unit, and four hunting areas (112-114, 115S) comprise the South Fork Shoshone herd unit (Fig. 30). Archery seasons occur in all herd units (Clarks Fork, North Fork Shoshone, and South Fork Shoshone) located near the eastern boundary of Yellowstone. Deer archery seasons, which open before rifle seasons, follow the same restrictions as the deer rifle seasons. In 1980, archery season for all three herds was only two weeks, from 16 to 30 September. In 1981 and 1982, seasons were two weeks long, however, several seasons opened 26 August and closed 9 September while others lasted from 16 to 30 September. From 1983 to 1987, archery seasons were lengthened to 1-30 September. Two hunting areas (115N and 115S) opened and closed 26 August and 9 September, respectively. In 1988 and 1989, archery seasons were the same for all hunting areas bordering the park and lasted from 1 to 30 September.

In 1980, general rifle season opening dates varied from 1 October to 15 October, and 1 November. All seasons closed 15 November. One rifle season (hunting area 115S) opened and closed dates of 10 September and 31 October, respectively. From 1981 to 1987, the general rifle season lasted from 1 October to 15 November for most hunting areas in the Clarks Fork and North and South Fork Shoshone herds. For some hunting areas, opening dates were later,

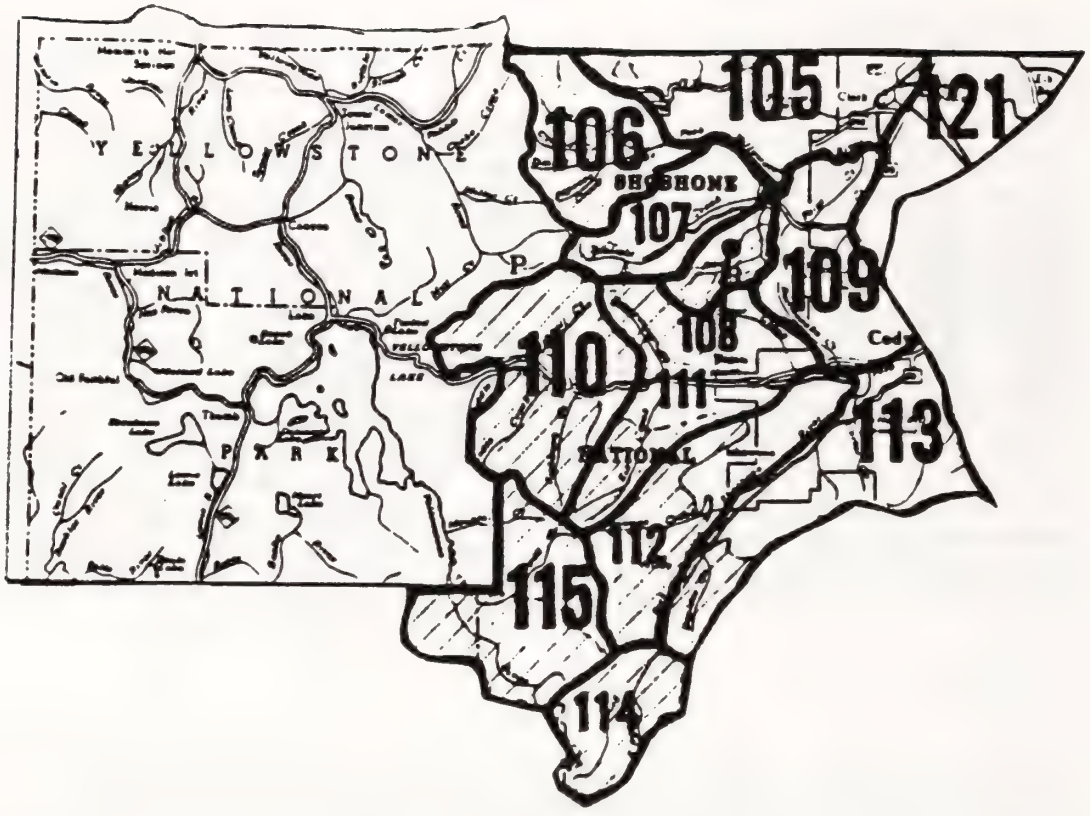


Fig. 30. Hunting area boundaries in District II, Wyoming for the Clarks Fork (hunting areas 105-109), North Fork Shoshone (hunting areas 110, 111, 115N), and South Fork Shoshone (hunting areas 112-114, 115S) mule deer herd units east of Yellowstone National Park.

beginning on 15 October or 1 November but these seasons still ended on 15 November. Hunting areas 115N and 115S had an earlier rifle season beginning 10 September and ending 31 October. In 1985, short antlerless or either-sex seasons were from 11 to 15 November. In 1986 and 1987, the antlerless/ either-sex season lasted from 10 to 15 November and 1 to 8 November, respectively. In response to public and outfitter pressure concerning the lack of trophy antlered bucks, only bucks with antlers having four points on at least one side could be legally harvested during the general season in 1988 and 1989. In 1988-1989, most seasons were shortened five days and lasted from 1 October to 10 November. The early seasons in hunting areas 115N and 115S were the same as in previous years (10 September-31 October) except for the addition of the four point rule. A short antlerless season (1-5 November) remained for some hunting areas and lasted from 1 to 5 November.

Special Permits

No special permits were issued in 1980. From 1981 to 1983, 550 either-sex permits were issued each year for all three herds (Clarks Fork, North Fork Shoshone, and South Fork Shoshone) combined. In 1984 only 500 either-sex permits were issued for the three herd units, and seasons for either-sex permits lasted from 1 to 15 November. After 1984, no either-sex permits were issued. Forty antlered permits (four points or more on one side) were issued in the South Fork Shoshone herd from 1982 to 1985. This season started 1 November and ended 30 November. Starting in 1986, antlered permits were issued only in the Clarks Fork herd (hunting area 109). One hundred permits were issued each year for this area through 1989. Season dates ran from 1 to 15 November.

Moose

The Crandall (hunting area 13), Sunlight (hunting area 12), North Fork Shoshone (hunting area 11), South Fork Shoshone (hunting area 31), and Thorofare (hunting area 8) moose herd units are located east of Yellowstone National Park (Fig. 31). Obtaining a special permit is the only way to legally hunt moose in Wyoming. Since 1980, only antlered bulls could be legally harvested from these five herd units.

From 1980 to 1987, opening dates for archery season began 26 August and ended 9 September for the Crandall, Sunlight, South Fork Shoshone, and Thorofare herds. Archery season opened later for the North Fork Shoshone herd (30 September) and ended 14 October for the years 1980-1987. Changes in opening dates and season lengths occurred for all herds in 1988. Opening dates for the Crandall, Sunlight, and Thorofare herds were set 11 days earlier to 15 August and closing dates remained at 9 September. Opening season dates for the North and South Fork Shoshone herds were later (1 September) and closed 30 September.

In 1980-1988, rifle season extended from 10 September to 15 November for the Crandall and Sunlight herds. The South Fork Shoshone herd had the same opening and closing dates as the Crandall and Sunlight herds from 1980 to 1987. In 1988, the South Fork season was shortened to 1 October-5 November. From 1980 to 1988, season opening and closing dates have remained the same for the North

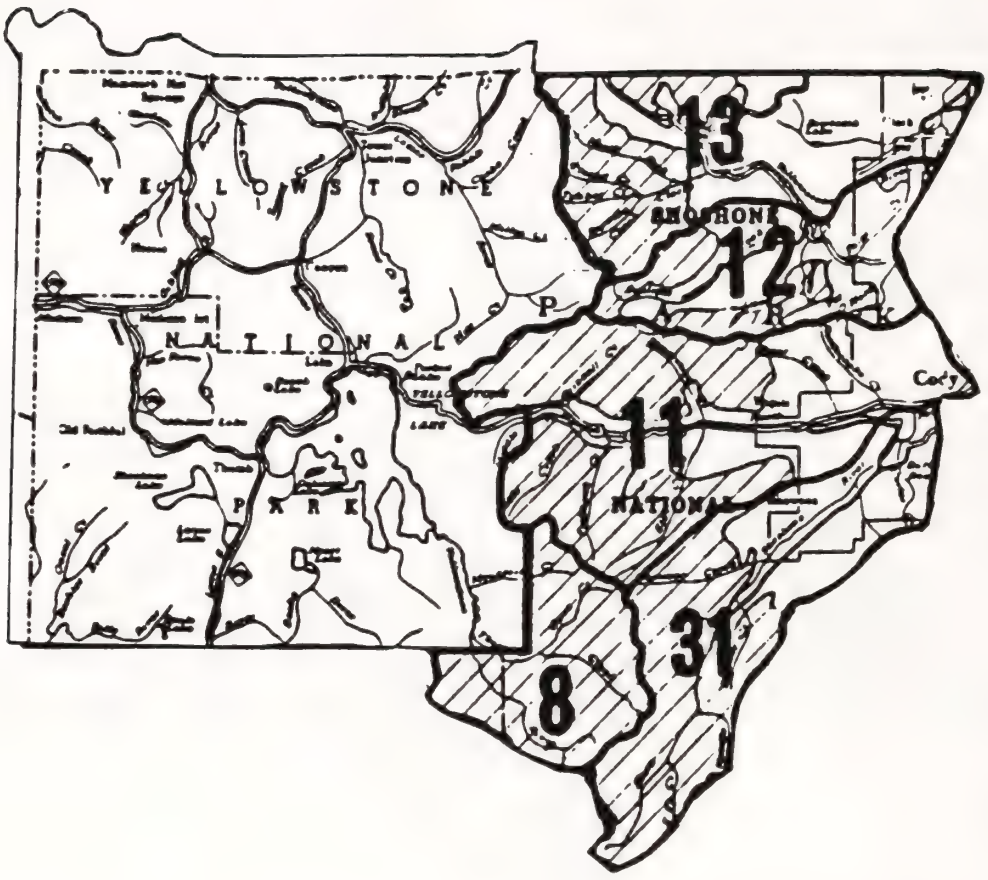


Fig. 31. Hunting area boundaries in District II, Wyoming for the Crandall (hunting area 13), Sunlight (hunting area 12), North Fork Shoshone (hunting area 11), South Fork Shoshone (hunting area 31), and Thorofare (hunting area 8) moose herd units east of Yellowstone Park.

Fork Shoshone herd, 15 October to 15 November respectively. Rifle season for the Thorofare has not changed from 1980 to 1989, beginning 10 September and ending 31 October.

Bighorn Sheep

The Clarks Fork (hunting area 1), Trout Peak (hunting area 2), Wapiti Ridge (hunting area 3), and Younts Peak (hunting area 4) bighorn sheep herd units east of Yellowstone National Park (Fig. 32). Special permits (from a drawing) are required to legally harvest bighorn sheep. Rams having a 3/4-or-larger curl horn are the only sheep that can be legally harvested in these four herd units.

The archery season lengths and dates varied slightly for four herds. From 1980 to 1987 archery season opened 17 August and closed 31 August. In 1988, the seasons for all four herds were lengthened with an opening date of 15 August and a closing date of 31 August.

Since 1980, rifle season has opened on 1 September and closed on 31 October for all four herds.

Harvest Summaries

Elk

Weather influences the timing and magnitude of elk migrations out of Yellowstone National Park for the Clarks Fork and North Fork Shoshone herds. Snow depths were significantly correlated with fall elk migrations (Rudd 1982, Rudd et al. 1983). As a result of variable snowfalls, harvests for the Clarks Fork and North Fork Shoshone elk herds have also been variable (Fig. 33, Table 15). Management strategies were implemented in the late 1980s to stabilize elk numbers for both of these herds (Hurley et al. 1988). Later hunting seasons, increased antlerless permits, and reduced hunting pressure on mature bulls were instituted. Increasing elk harvests on migratory segments (from Yellowstone N.P.) while reducing harvests of resident herd segments has complicated the management of the Clarks Fork and North Fork Shoshone elk herds.

Elk harvests from the Clarks Fork and North Fork Shoshone herds increased dramatically from 1980 to 1982 and remained relatively stable until 1987. Average total harvest and hunter success from 1982 to 1986 was 713 (32% success) and 570 (31% success) for the Clarks Fork and North Fork herds, respectively (Table 15). The low harvest in 1987 was due to mild winter weather conditions. The harvest for both herds again increased in 1988 due to the greater Yellowstone area fires and more normal winter weather conditions.

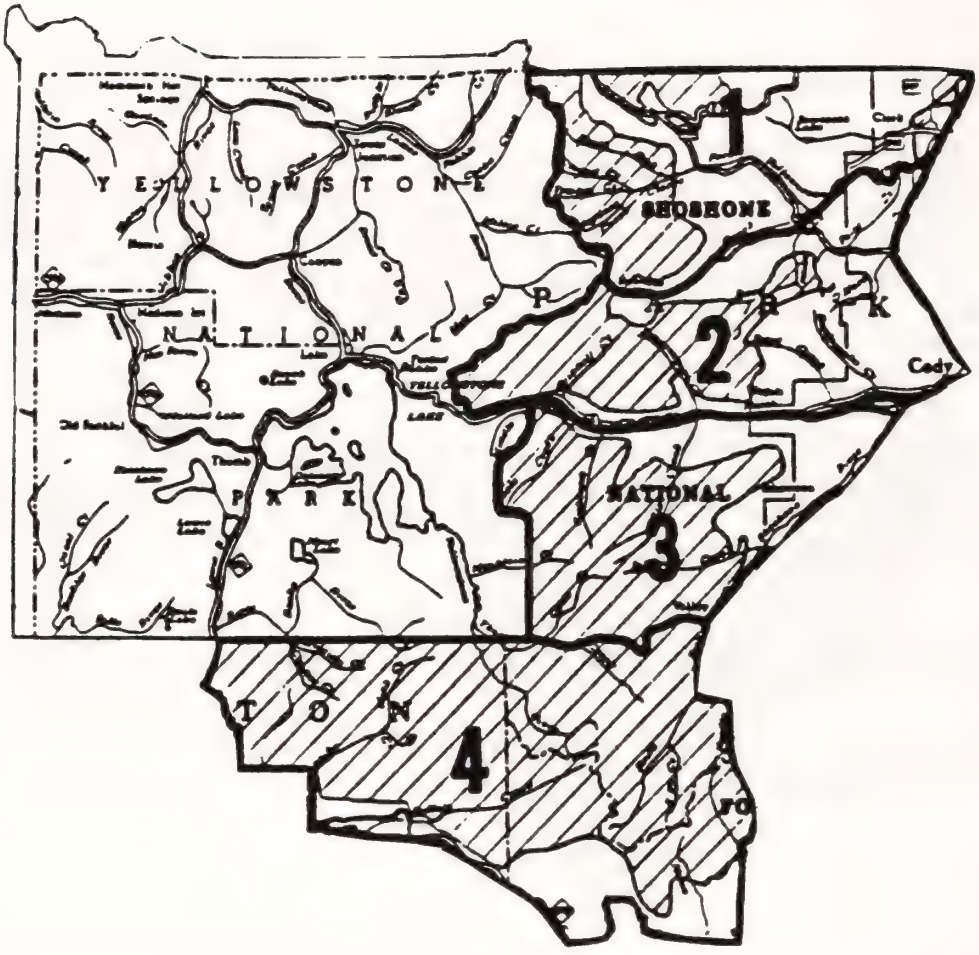


Fig. 32. Hunting area boundaries in District II, Wyoming for the Clarks Fork (hunting area 1), Trout Peak (hunting area 2), Wapiti Ridge (hunting area 3), and Yount's Peak (hunting area 4) bighorn sheep herd units east of Yellowstone National Park.

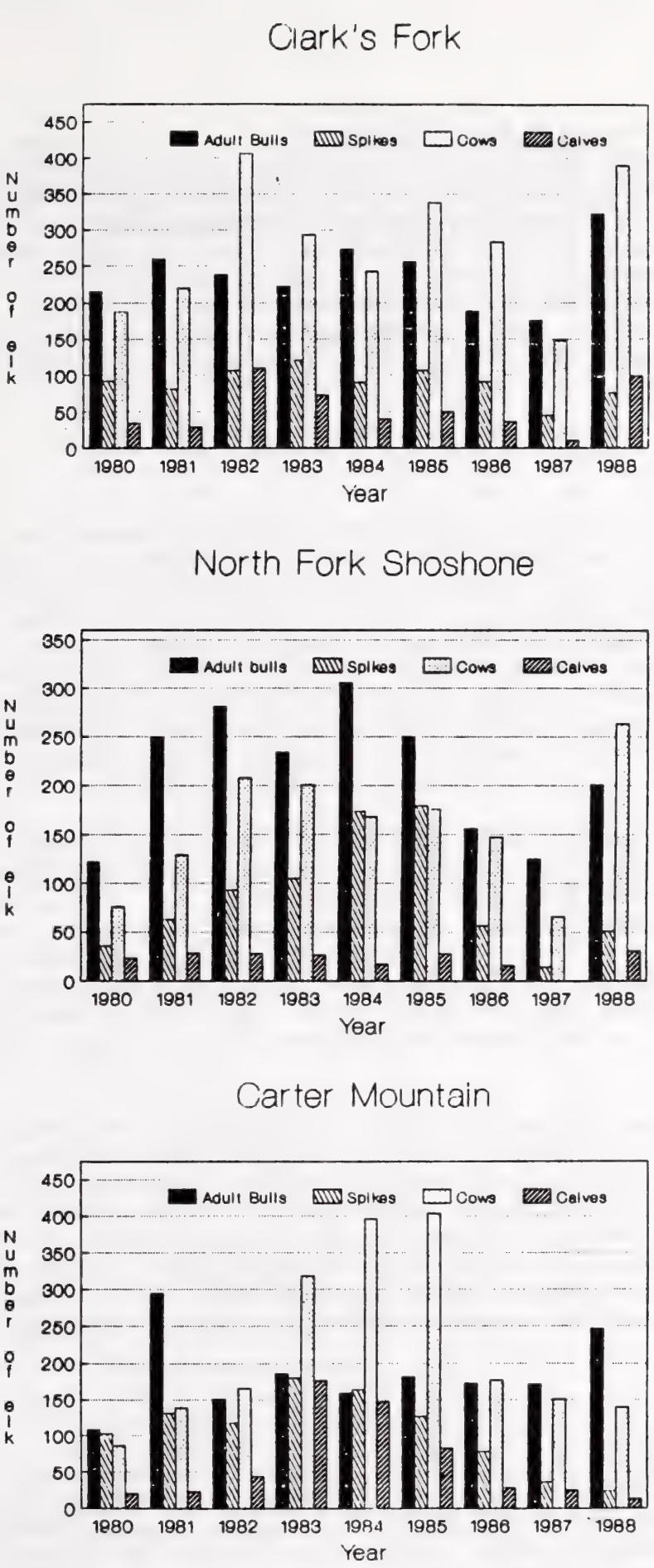


Fig. 33. Number of adult and spike bulls, cows and calves harvested from the Clarks Fork, North Fork Shoshone, and Carter Mountain elk herds in Wyoming east of Yellowstone National Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

The Carter Mountain herd apparently has a few migrating elk from Yellowstone. In 1989, migrating elk were tracked in the snow from the Thorofare area of Yellowstone National Park to Carter Mountain (South Fork Shoshone) winter ranges (F. J. Singer pers. comm.). No radiotelemetry studies have been conducted on this herd. A study is planned in 1990 to trap and radiocollar elk to more accurately determine seasonal movements of this herd. Annual harvest increased from 1980 to 1983 (average harvest of 461 elk), remained relatively high from 1983 to 1985 (average harvest of 787 elk), and then dropped and remained stable from 1986 to 1988 (average harvest of 421 elk, Table 15).

Mule Deer

From 1980 to 1988, the average annual deer harvests (and percent hunter success) for the Clarks Fork, North Fork Shoshone, and South Fork Shoshone herds were 565 (31% success), 242 (27% success), 792 (44% success), respectively (Table 16). Total harvests for the Clarks Fork and North Fork and South Fork Shoshone herds were relatively stable to slightly increasing through 1985 (Fig. 34). The harvest declined from 1986 through 1988 for the Clarks Fork and South Fork Shoshone herds. The decline in the 1987 harvest was partly due to the drier fall weather (Hurley et al. 1988). The harvest for the North Fork Shoshone herd declined in 1988 compared to the previous five years (Fig. 34).

Bucks dominated the mule deer harvest from 1980 to 1987 for all three herds (Fig. 35). In 1988, nearly 1.3 times more does than bucks were harvested in the Clarks Fork and South Fork Shoshone herds. Doe and buck harvests in the North Fork Shoshone herd were nearly equal (81 and 85, respectively) for 1988. The change in buck harvest was due to new hunting regulations only allowing harvest of bucks with at least one antler of four points or more. In 1988, the four point rule and a five day reduction in the general season length contributed to the lowest deer harvest in nine years for all herds.

The increased doe harvest, particularly since 1986, was influenced by the elimination of either-sex permits in 1985 (Fig. 35), the beginning of a short antlerless or either-sex general hunting season, and a restriction allowing harvest of four points or larger bucks in 1988. These changes have all been designed to reduce the buck harvest (Yorgason et al. 1985, 1986; Hurley et al. 1988). The age structure (from cementum annuli aging) of harvested mule deer heavily favors yearling and 2-year-old bucks for all three herds (Table 17). The female harvest appears more evenly distributed among all age classes.

Moose

Since 1980, moose harvests along Yellowstone National Park's eastern border have remained relatively stable and consisted almost entirely of bulls (Table 18). The exception was in 1980 when one calf was harvested in the Thorofare area. Hunters in the Crandall area have enjoyed nearly 100% success (average of 96% from 1980 to 1988) although the number of permits increased from five to ten animals starting in 1981. Harvests and success rates have remained constant for the Sunlight area at five bulls and 100%, respectively (Table 18).

Table 15. Elk harvest questionnaire summaries for herd units east of Yellowstone National Park in District II, Wyoming, 1980-1988 (from Yorgason et al. 1981-1987, Hurley et al. 1988, 1989).

Herd	Hunting Areas	Year	Number of Hunters	Sex and age composition: Yearling Bulls	Adult Bulls	Cows	Calves	Total	Percent Success
Clarks Fork[a]	50-54,	1980	2653	92	215	188	34	532	19.8
	121	1981	2847	81	260	220	29	590	21.0
		1982	2307	106	238	406	109	859	37.2
		1983	2273	120	223	294	72	709	31.2
		1984	2153	90	273	243	40	646	30.0
		1985	2383	106	256	338	50	750	31.5
		1986	1923	91	189	284	36	600	31.2
		1987	1804	45	176	148	10	379	21.0
		1988	1914	75	322	389	98	884	46.2
North Fork Shoshone	55-60N	1980	1300	36	122	76	23	257	22.6
		1981	1896	63	249	129	29	470	29.1
		1982	1824	93	281	208	28	610	33.4
		1983	1723	105	234	201	27	567	32.9
		1984	2095	174	306	168	18	666	31.8
		1985	2126	179	250	176	28	633	29.8
		1986	1749	57	156	147	16	376	26.1
		1987	1432	15	125	66	0	206	14.4
		1988	1346	51	201	263	31	546	40.6
South Fork Shoshone	57-60S	1980	1342	103	108	86	21	318	22.5
Carter Mt.[b]	58,59,								
	60S,61	1981	1853	131	295	139	23	588	32.6
		1982	1563	117	151	165	44	477	30.5
		1983	2229	180	186	319	17	702	31.5
		1984	2354	164	159	396	147	866	36.8
		1985	2235	127	181	404	82	794	35.5
		1986	1499	78	172	177	28	455	30.4
		1987	1506	36	171	151	25	383	25.4
		1988	1164	24	247	140	13	424	36.4

[a] New hunting area 121 was added in 1986.

[b] In 1981 herd unit boundaries were changed during the project year to include Hunt Area 61 and to exclude Hunt Unit 57. This was done after a review of data collected from tagging, banding, and radio collaring work done in the 1960s and again in recent years Unit 57 was included in the Clarks Fork herd. Along with the herd unit boundary changes noted above, the herd name was changed from South Fork Shoshone to Carter Mountain.

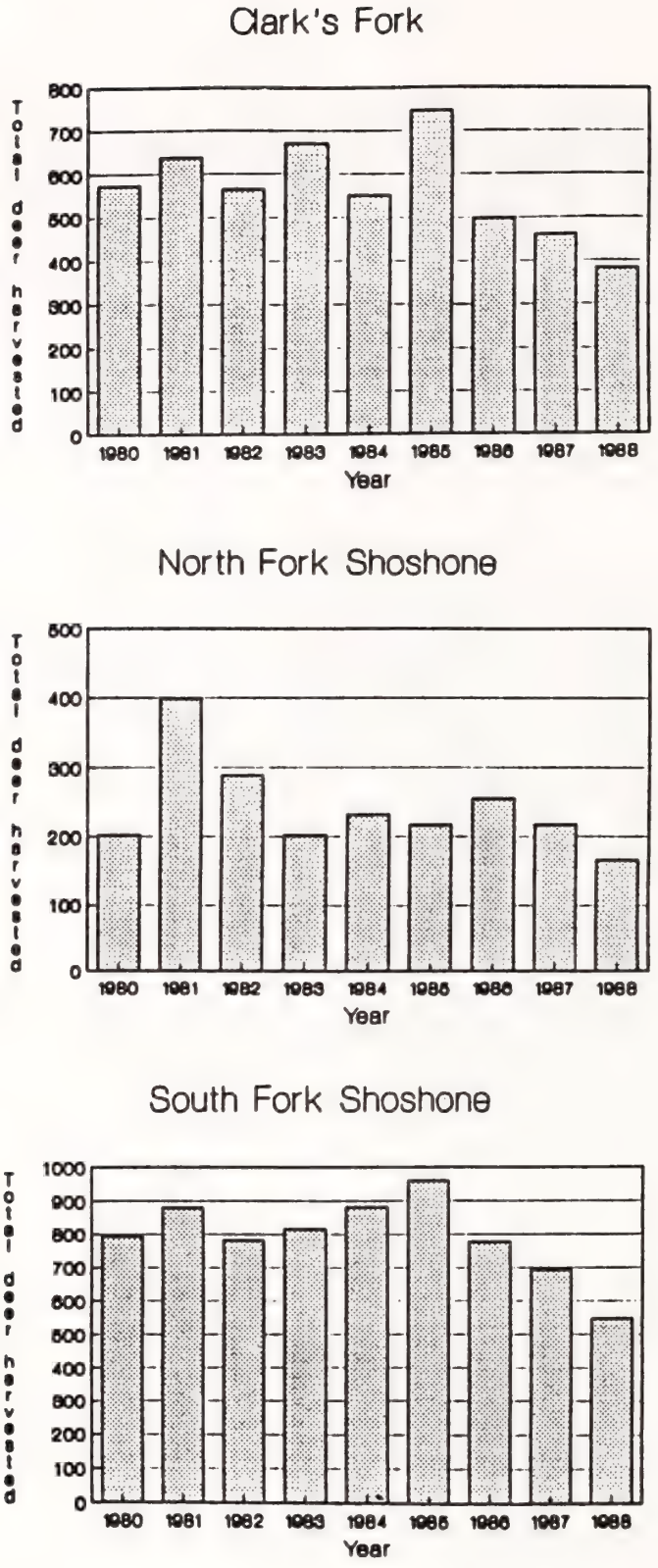


Fig. 34. Total number of mule deer harvested in the Clarks Fork, North Fork Shoshone, and South Fork Shoshone herd units in Wyoming east of Yellowstone National Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

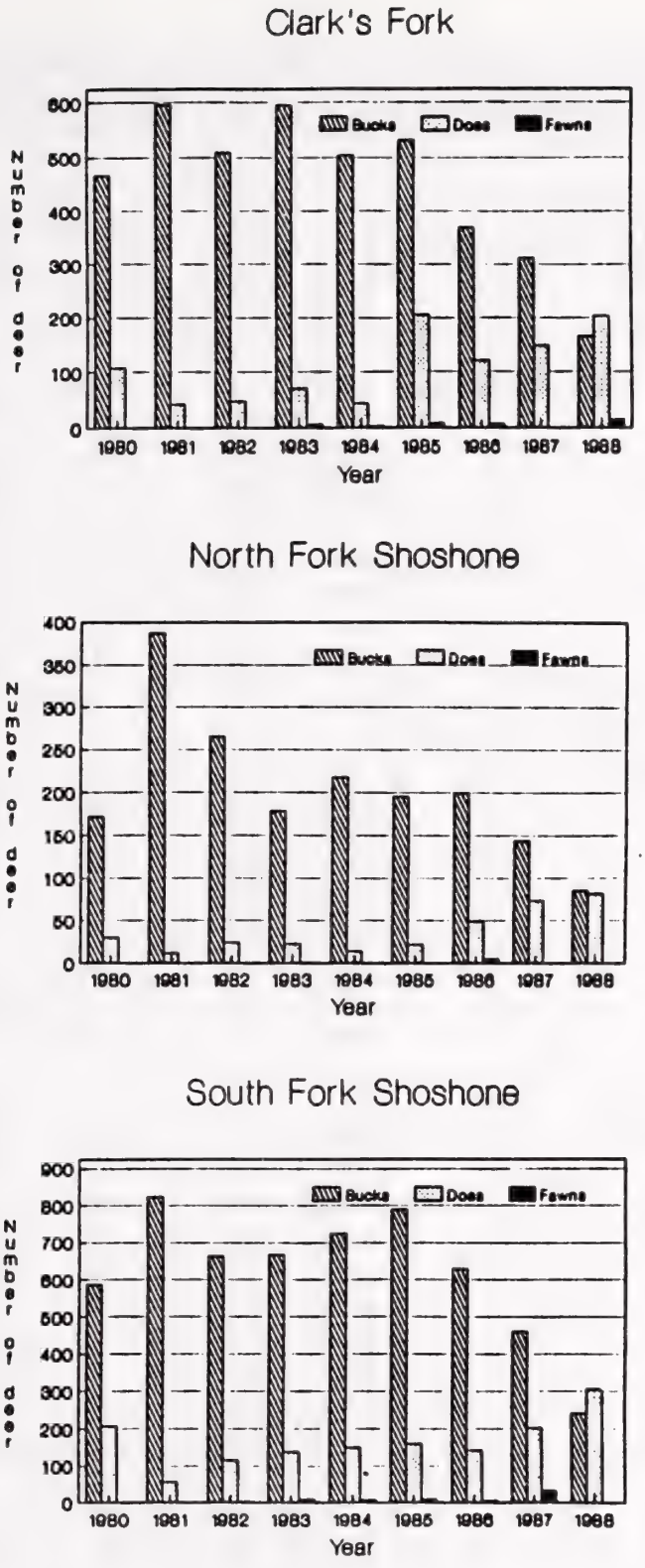


Fig. 35. Number of bucks, does, and fawns harvested in the Clarks Fork, North Fork Shoshone, and South Fork Shoshone mule deer herd units in Wyoming east of Yellowstone National Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

Table 16. Mule deer harvest questionnaire summaries for herd units east of Yellowstone National Park in District II, Wyoming, 1980-1988 (from Yorgason et al. 1981-1987; Hurley et al.1988, 1989).

Herd	Hunting Areas	Year	Number of Hunters	Sex and age composition				Percent Success
				Bucks	Does	Fawns	Total	
Clarks Fork	105-109	1980	2599	467	107	-	574	19.2
		1981	2247	596	41	-	637	22.4
		1982	2030	509	47	-	564	27.8
		1983	1926	596	69	6	671	34.8
		1984	1634	504	43	3	550	33.7
		1985	1799	532	206	9	747	41.5
		1986	1530	369	121	8	498	32.5
		1987	1404	312	148	-	460	32.8
		1988	1198	165	203	15	383	32.0
North Fork Shoshone	110,111, 115N	1980	921	172	30	-	202	18.5
		1981	1357	387	12	-	399	25.3
		1982	1148	265	24	-	289	25.2
		1983	891	178	23	1	202	22.7
		1984	802	218	14	-	232	28.9
		1985	669	195	22	-	217	32.4
		1986	761	200	49	6	255	33.5
		1987	727	144	73	-	217	29.8
		1988	643	85	81	-	166	25.8
South Fork Shoshone	112-115S	1980	2117	586	208	-	794	29.6
		1981	2037	823	56	-	879	35.0
		1982	1922	663	116	2	781	39.9
		1983	1820	667	139	10	816	44.8
		1984	1716	725	150	7	882	56.8
		1985	1690	790	160	10	960	56.8
		1986	1600	630	142	6	778	48.6
		1987	1687	460	202	32	694	41.1
		1988	1346	242	306	-	548	40.7

Table 17. Age structure of mule deer harvested in District II, Wyoming east of Yellowstone National Park, 1980-1986 (adapted from Hurley et al. 1988). Ages were determined by cementum annuli aging.

Herd	Year	Sex	Numbers in age class									
			Fawns	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	>8.5
Clarks Fork	1980	Male	0	28	11	12	2	3	0	0	0	0
		Female	0	5	1	4	4	3	0	0	0	0
	1981	Male	0	73	45	11	4	2	1	0	0	2
		Female	0	3	2	0	3	0	1	0	0	0
	1982	Male	0	42	16	14	5	1	2	0	0	1
		Female	0	5	2	1	1	1	0	0	0	0
	1983	Male	1	65	25	25	5	0	4	4	0	1
		Female	1	3	4	2	1	0	0	0	1	1
	1984	Male	0	33	33	15	11	5	0	1	1	0
		Female	0	3	0	1	1	1	0	0	2	1
	1985	Male	0	50	23	15	12	5	2	1	3	1
		Female	2	3	0	1	3	7	5	1	1	5
	1986	Male	3	28	31	13	4	0	1	1	0	0
		Female	4	2	2	0	3	3	1	0	0	2
North Fork Shoshone	1980	Male	0	28	4	9	6	2	0	0	0	0
		Female	0	2	3	2	1	1	0	0	0	0
	1981	Male	1	52	24	13	1	3	0	1	0	1
		Female	0	2	1	0	0	0	0	0	1	0
	1982	Male	0	46	18	9	2	2	1	0	0	1
		Female	0	0	1	3	0	0	3	0	0	4
	1983	Male	0	23	17	12	2	2	2	0	0	0
		Female	1	0	2	1	1	0	0	1	0	2
	1984	Male	0	21	21	6	2	1	2	0	2	0
		Female	0	0	2	1	0	0	0	0	0	0
	1985	Male	0	24	17	8	4	0	3	0	0	0
		Female	0	1	0	2	0	0	3	1	0	1
	1986	Male	0	28	22	7	2	0	0	1	0	0
		Female	1	3	1	0	0	1	0	2	2	0

Table 17. Continued.

Herd	Year	Sex	Numbers in age class									
			Fawns	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	>8.5
South Fork Shoshone												
	1980	Male	0	121	35	33	21	6	0	0	0	0
		Female	0	9	4	7	2	12	0	0	0	0
	1981	Male	0	83	51	33	23	5	1	1	0	0
		Female	4	4	6	3	2	2	1	1	1	2
	1982	Male	0	102	37	29	7	0	1	0	0	0
		Female	1	7	9	5	4	1	3	0	1	2
	1983	Male	2	69	53	23	9	2	2	3	0	0
		Female	2	9	5	4	1	0	2	1	0	4
	1984	Male	0	60	47	20	10	4	1	0	0	0
		Female	0	7	6	5	6	6	0	0	0	0
	1985	Male	3	81	58	32	15	5	4	0	0	1
		Female	1	7	11	9	5	8	2	1	2	6
	1986	Male	3	61	80	43	11	5	2	0	0	1
		Female	1	2	9	5	4	4	6	3	2	4

Table 18. Moose harvest questionnaire summaries for herd units east of Yellowstone National Park in District II, Wyoming, 1980-1988 (from Yorgason et al. 1981-1987; Hurley et al. 1988, 1989).

Herd	Hunting Area	Year	Number of Permits	Number of Hunters	Total Bulls	Percent Success
Thorofare	8	1980	35	33	26[a]	78.5
		1981	35	31	25	80.6
		1982	35	32	25	78.1
		1983	30	28	23	82.1
		1984	30	29	20	69.0
		1985	30	29	20	69.0
		1986	25	21	20	95.0
		1987	25	25	24	96.0
		1988	25	23	21	91.3
North Fork Shoshone	11	1980	5	5	5	100.0
		1981	5	5	4	80.0
		1982	5	5	2	40.0
		1983	5	5	3	60.0
		1984	5	4	2	50.0
		1985	5	5	4	80.0
		1986	5	5	2	40.0
		1987	5	5	5	100.0
		1988	5	5	4	80.0
Sunlight	12	1980	5	5	5	100.0
		1981	5	5	5	100.0
		1982	5	5	5	100.0
		1983	5	5	5	100.0
		1984	5	5	5	100.0
		1985	5	5	5	100.0
		1986	5	5	5	100.0
		1987	5	5	5	100.0
		1988	5	5	5	100.0
Crandall	13	1980	5	4	4	100.0
		1981	10	10	10	100.0
		1982	10	10	10	100.0
		1983	10	10	10	100.0
		1984	10	10	10	100.0
		1985	10	10	10	100.0
		1986	10	10	10	100.0
		1987	10	10	10	100.0
		1988	10	10	6	60.0

Table 18. Continued.

Herd	Hunting Area	Year	Number of Permits	Number of Hunters	Total Bulls	Percent Success
South Fork Shoshone	31	1980	5	4	3	66.6
		1981	5	5	5	100.0
		1982	5	5	1	25.0
		1983	5	5	4	80.0
		1984	5	4	1	25.0
		1985	5	5	5	100.0
		1986	5	5	3	75.0
		1987	5	5	4	80.0
		1988	5	5	4	80.0

[a] Includes one calf in the total.

Despite this high success, biologists are taking a conservative approach to harvests due to many factors including lack of management data, illegal kills, and habitat changes on private land (Yorgason et al. 1984, 1985). The harvests and success rates in the North Fork Shoshone and South Fork Shoshone herds have been quite irregular due in part to the marginal habitat, the large amount of effort required to bag a moose, and the dispersed nature of moose in these areas (Fig. 36). Moose in the Thorofare area have received the most attention and management changes. Concerns that the herd was declining were expressed as early as 1981 (Yorgason et al. 1981). Hunters were also concerned about the lack of trophy bulls in the area (Yorgason et al. 1983). These concerns have led to a reduction in the number of permits issued from 35 in 1980 to 24 in 1988. Total harvest of bulls, however, has not declined appreciably.

Bighorn Sheep

Bighorn sheep harvests east of Yellowstone National Park have been relatively stable to slightly increasing (Fig. 37). The unusually low harvest and hunter success for the Clarks Fork herd in 1988 was primarily due to forest fires in that area. Average annual harvest of rams (1980-1988) is 13 for the Clarks Fork (14 when excluding the 1988 data), 19 for Trout Peak, 28 for Wapiti Ridge, and 31 for Younts Peak (Table 19). Average ages of rams harvested varies between herds and ranges between 5 and 7.9 years (Table 20).

Wapiti Ridge is the only area having an increase in the number of available permits from 1980 to present. The increases in 1984 to 36 permits and in 1986 to 40 permits followed the Wyoming Game and Fish Department's belief that herd numbers were increasing and could support an increased harvest (Yorgason et al. 1983). Total rams harvested subsequently increased (Fig. 37).

Hunter success has varied for all herds. Average annual hunter success (1980-1988) is 54.6% (59.9% excluding 1988 data), 59.9%, 78.9%, and 53.1% for the Clarks Fork, Trout Peak, Wapiti Ridge, and Younts Peak herds, respectively (Table 20). Hunter success on Wapiti Ridge is the highest of any area east of Yellowstone National Park and may be related to relatively easy access to sheep range compared to other areas. Since 1986, some of the high success rates have been biased by bighorn sheep hunters holding complimentary sheep hunting licenses, allowing them to hunt in any sheep hunting area. A complimentary license holder is only recorded as hunting if that hunter bags a sheep. Thus hunter success rates for complimentary license holders are always recorded as 100%. This fact has the effect of artificially increasing the reported hunter success.

Population Trends

Elk

Elk numbers have steadily increased in the Clarks Fork, North Fork Shoshone, and Carter Mountain herds (Fig. 38). Elk population estimates in Wyoming are derived from a computer model using winter range classification counts (Table 21).

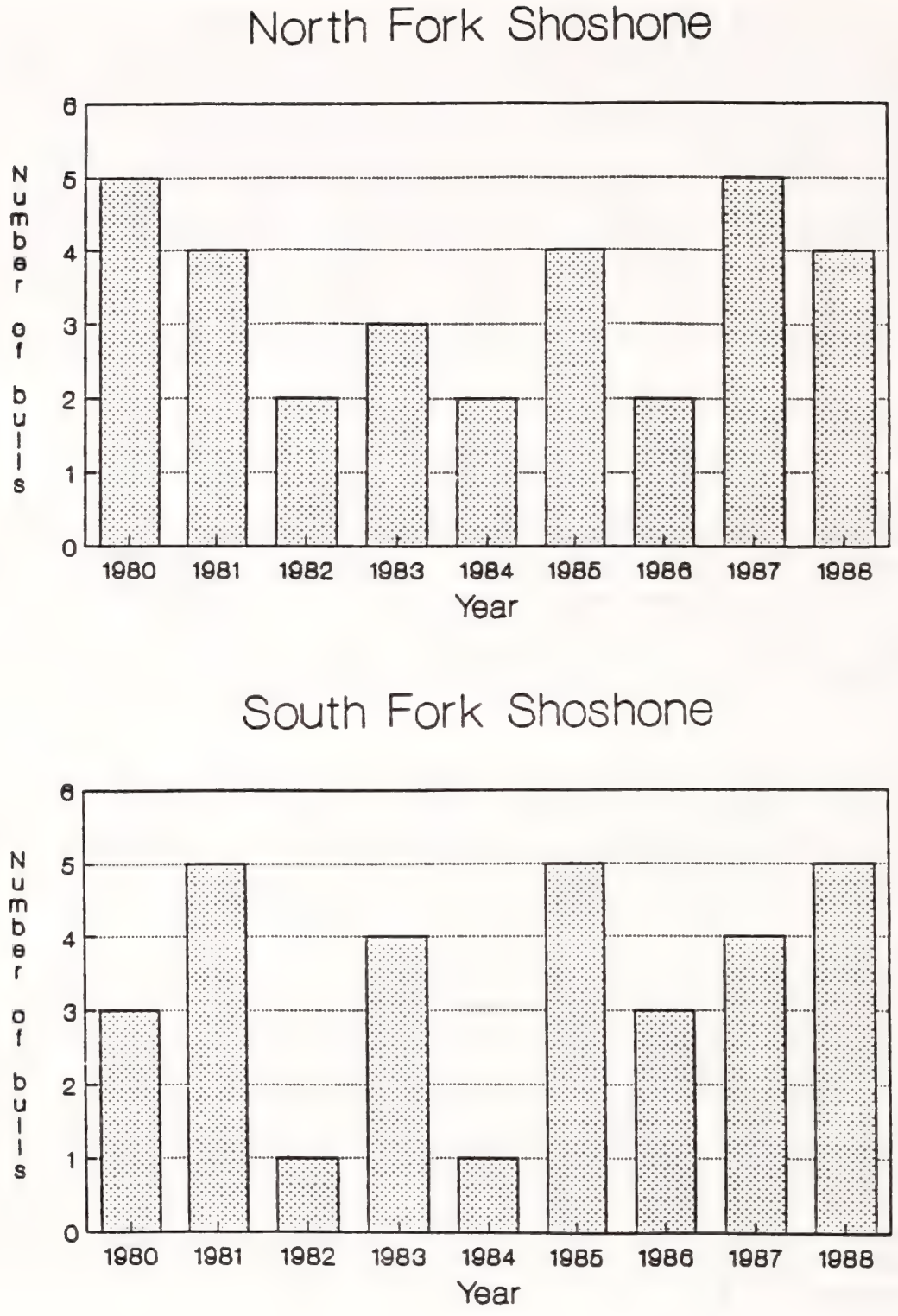


Fig. 36. Number of bull moose harvested from the North Fork and South Fork Shoshone herd units in Wyoming east of Yellowstone Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

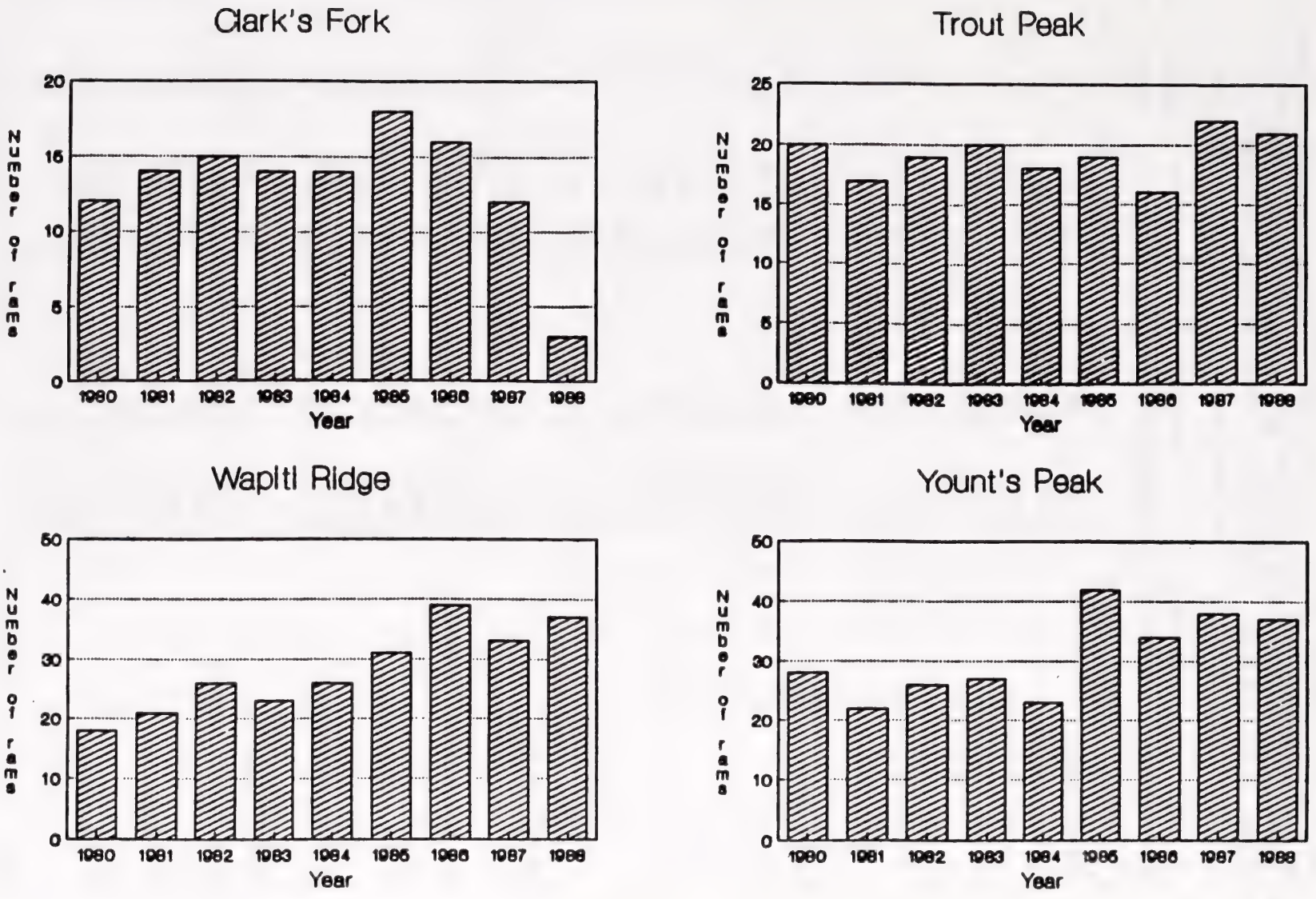


Fig. 37. Number of bighorn sheep rams harvested from the Clark's Fork, Trout Peak, Wapiti Ridge, and Yount's Peak herd units in Wyoming east of Yellowstone Park, 1980-1988 (adapted from Yorgason et al. 1981-1987; Hurley et al. 1988, 1989).

Table 19. Bighorn sheep harvest summaries for herd units east of Yellowstone National Park in District II, Wyoming, 1980-1988. (Adapted from Yorgason et al. 1981-1987), Hurley et al. 1988-1989).

Herd	Hunting Area	Year	Number of Permits	Number of Hunters	Total Rams	Percent Success
Clarks Fork	1	1980	24	24	12	50.0
		1981	24	23	14	60.8
		1982	24	24	15	62.5
		1983	24	24	14	58.3
		1984	24	24	14	58.3
		1985	24	24	18	75.0
		1986	24	25[a]	16	64.0
		1987	24	24	12	50.0
		1988	24	24	3	12.5
Trout Peak	2	1980	32	--	16	----
		1981	32	32	17	53.1
		1982	32	32	19	59.4
		1983	32	32	20	62.5
		1984	32	31	18	58.1
		1985	32	32	19	59.4
		1986	32	31	16	51.6
		1987	32	33[a]	22	66.7
		1988	32	32[a]	21	65.6
Wapiti Ridge	3	1980	32	31	18	58.1
		1981	32	32	21	65.6
		1982	32	32	26	81.3
		1983	32	31	23	74.2
		1984	36	36	26	72.2
		1985	36	36	31	86.1
		1986	40	40[b]	39	97.5
		1987	40	40	33	82.5
		1988	40	40[c]	37	92.5
Younts Peak	4	1980	60	60	28	46.7
		1981	60	54	22	40.7
		1982	60	60	26	81.3
		1983	60	59	27	45.8
		1984	60	57	23	40.4
		1985	60	58	42	72.4
		1986	60	57	34	59.6
		1987	60	57	38	66.7
		1988	60	59	37	62.7

[a] Includes 1 complimentary license holder.
[b] Includes 5 complimentary license holders.
[c] Includes 4 complimentary license holders.

Table 20. Ages of bighorn rams harvested in the Clarks Fork, Trout Peak, Wapiti Ridge, and Younts Peak herds in District II, Wyoming east of Yellowstone National Park, 1980-1988.[a] Ages are from cementum annuli of incisors.

Herd	Year	Number at age 2	3	4	5	6	7	8	9	10	11	12	13	Average Age
Clarks Fork	1980	--	--	--	1	--	2	1	1	--	--	--	--	7.7
	1981	--	--	--	4	1	1	--	--	--	--	--	--	6.0
	1982	--	--	2	2	1	--	1	--	--	--	--	--	5.8
	1983	--	--	1	2	1	1	1	--	--	--	--	--	7.0
	1984	--	--	--	1	2	--	1	--	--	--	--	--	6.3
	1985	--	--	--	2	3	2	2	--	--	--	--	--	6.4
	1986	--	--	--	1	1	4	--	--	--	--	--	--	6.5
	1987	--	--	--	2	1	1	--	--	1	1	--	--	7.3
Trout Peak	1980	--	--	1	4	2	--	--	--	--	--	--	--	5.6
	1981	--	1	--	7	1	--	1	--	--	--	--	--	5.7
	1982	--	2	1	6	1	2	--	--	--	--	--	--	5.5
	1983	--	--	4	3	2	1	1	1	--	--	--	--	5.6
	1984	--	--	3	2	4	--	1	--	--	--	--	--	5.4
	1985	--	1	1	2	4	4	1	--	--	--	--	--	5.9
	1986	--	--	1	1	2	5	--	--	1	--	--	--	6.6
	1987	--	--	1	1	5	3	1	--	--	1	--	--	6.6
	1988	--	--	--	5	4	2	1	1	1	--	--	--	6.4
Wapiti Ridge	1980	--	--	--	2	2	1	--	--	1	--	--	--	7.0
	1981	--	--	1	1	2	1	--	--	--	--	--	--	6.1
	1982	--	1	5	3	1	2	--	1	--	--	--	--	5.6
	1983	--	--	1	2	4	4	1	--	--	--	--	--	6.2
	1984	--	--	3	--	2	6	5	1	--	1	--	--	7.0
	1985	--	--	4	7	2	5	2	--	--	1	--	--	6.9
	1986	1	2	--	5	6	5	4	2	--	--	--	--	6.2
	1987	--	--	--	4	3	3	2	2	--	2	--	--	7.2
	1988	--	--	--	3	6	3	2	2	3	1	--	2	7.9
Younts Peak	1980	--	--	--	2	1	--	1	--	--	--	--	--	6.0
	1981	--	--	--	2	--	--	--	--	--	--	--	--	5.0
	1982	--	--	1	1	1	--	--	--	--	--	--	--	5.0
	1983	--	--	--	--	1	1	--	--	--	--	--	--	6.5
	1984	--	--	1	2	2	3	1	1	--	--	--	--	6.4
	1985	--	--	--	2	7	2	--	2	1	--	--	--	6.7
	1986	--	--	2	1	--	--	1	--	--	--	--	--	5.3

[a] Data adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988-1989).

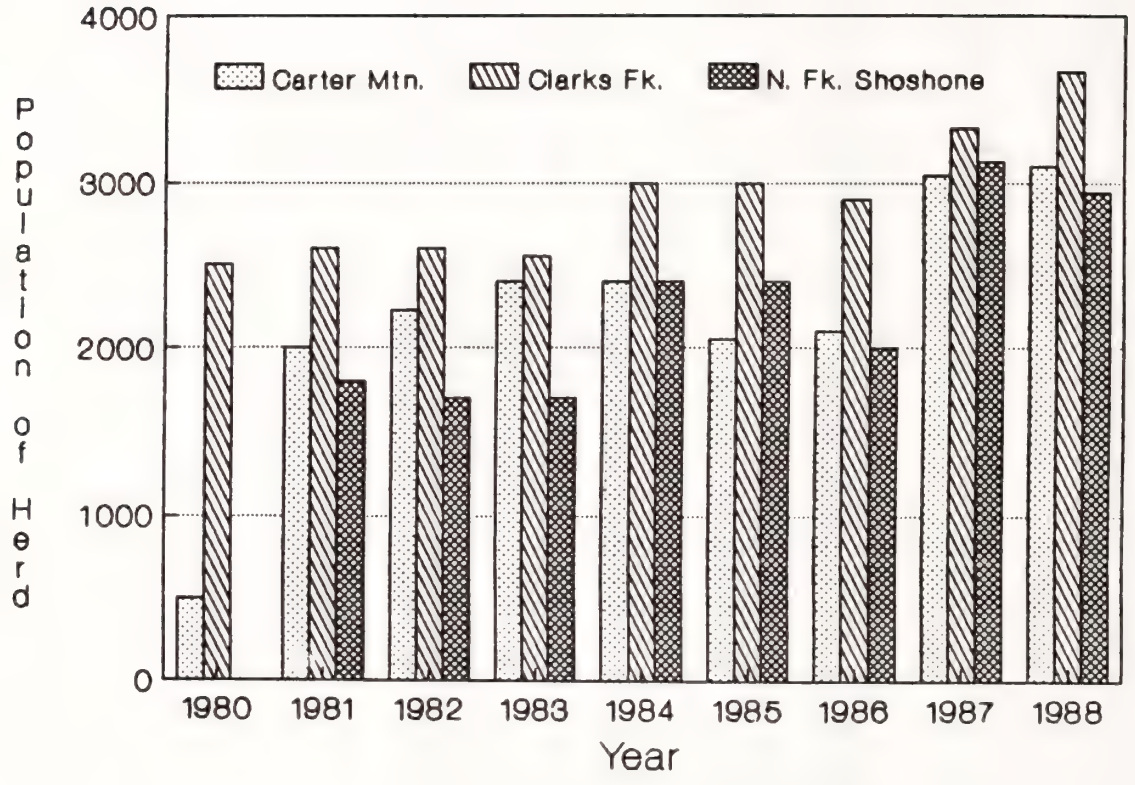


Fig. 38. Estimated numbers of elk for the Clarks Fork, North Fork Shoshone, and Carter Mountain herd units in Wyoming east of Yellowstone National Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

The greatest population increases have occurred in the Carter Mountain and North Fork Shoshone herds, both increasing an estimated 1,000 animals beginning in 1987 (Table 22). The Clarks Fork herd averaged 2,563 elk from 1980 to 1983, then increased to an average of 3,180 from 1984 to 1988. Recruitment as measured in calves/100 cows has been relatively stable since 1980 for all three herds (Fig. 39), averaging 40 calves/100 cows for Carter Mountain, 38 calves/100 cows for Clarks Fork (excluding year 1982 because of low sample size) and 37 calves/100 cows for North Fork Shoshone (1980 was excluded because of small sample size).

Deer

Mule deer population numbers for the Clarks Fork, North Fork Shoshone, and South Fork Shoshone have been stable or slightly increasing (Table 23). Numbers of deer are estimated from a computer model. The computer models consistently overestimated population numbers, sometimes by a factor of two ,of what biologists believed were in the herd. Bucks/100 does in postseason classifications were low (Table 24). This would be expected due to the heavy harvest of bucks compared to does from 1980 to 1987 (Table 25). However, the buck to doe ratio changed substantially in 1988 due to implementation of a the four-point or larger restriction.

Moose

The Thorofare herd unit contains the best moose habitat in District II and probably has more moose than the Crandall, Sunlight, North Fork Shoshone and South Fork Shoshone herd units combined. Recent loss of riparian willow habitat on private land in the Sunlight herd unit may limit this herd's population (Hurley et al. 1988). The North and South Fork Shoshone river areas support marginal moose habitat (Yorgason et al. 1982, 1983, 1986). Population models have not been developed for any of the herd units because classification and trend data were not collected.

Bighorn Sheep

Bighorn sheep populations for the Clarks Fork, Trout Peak, Wapiti Ridge, and Younts Peak herds have been slightly increasing from 1980 to 1987. No population model exists for the Clarks Fork herd but numbers are believed stable at approximately 500 animals (Table 26). Management data are lacking for this herd (Yorgason et al. 1987). Postseason classification data for this herd is incomplete, precluding trend comparisons.

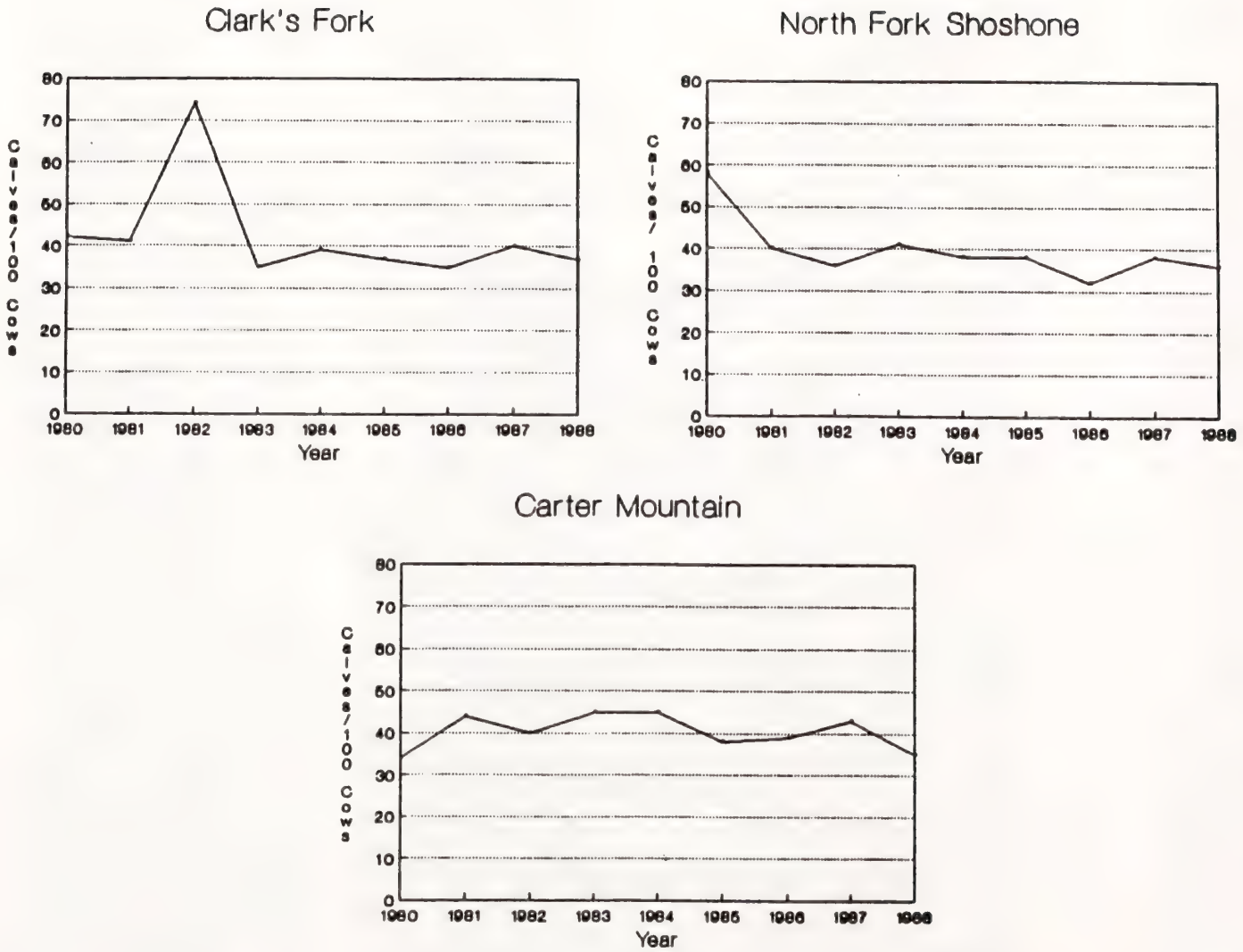


Fig. 39. Elk recruitment, measured in calves/100 cows, for the Clarks Fork, North Fork Shoshone, and Carter Mountain herd units in Wyoming east of Yellowstone Park, 1980-1988 (adapted from Yorgason et al. 1981-1987 and Hurley et al. 1988, 1989).

Table 21. Population classifications for elk in District II, Wyoming east of Yellowstone National Park, 1980-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd	Hunt area	Year	Calves 100 Cows	Bulls/ 100 Cows[a]	Ylng. Bull/ 100 Cows	Number Classified
Carter Mountain[b]	57-59,60S, 58,59,60S, 61	1980	34	6	0	287
		1981	44	7	5	85
		1982	40	6	4	605
		1983	45	7	5	207
		1984	45	9	7	1158
		1985	38	8	7	704
		1986	39	13	9	1076
		1987	43	14	13	987
		1988	35	16	14	1078
Clarks Fork	50-54	1980	42	13	7	271
		1981	41	5	2	826
		1982	74	62	0	64
		1983	35	7	4	742
		1984	39	5	2	872
		1985	37	11	5	810
		1986	35	7	1	2133
		1987	40	13	6	1762
		1988	37	9	6	1267
North Fork Shoshone	55,56,60N	1980	58	10	8	78
	55-57,60N[c]	1981	40	7	6	345
		1982	36	7	6	491
		1983	41	6	2	311
		1984	38	6	5	741
		1985	38	9	3	551
		1986	32	6	5	718
		1987	38	8	7	949
		1988	36	9	5	974

[a] Includes total for mature and yearling bulls.

[b] In 1980 this herd unit was identified as South Fork Shoshone. In 1981 the herd was renamed Carter Mountain and the boundaries expanded to include hunt area units 58, 59, 60S, and 61.

[c] In 1981 the North Fork Shoshone herd was expanded to include hunt area 57.

Table 22. Winter population estimates for 3 elk herds in District II, Wyoming east of Yellowstone National Park, 1980-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Year	Population Estimate		
	Carter Mountain	Clarks Fork	North Fk. Shoshone
1980	500	2500	---
1981[a]	2000	2600	1800
1982	2225	2600	1700
1983	2400	2550	1700
1984	2400	3000	2400
1985	2050	3000	2400
1986[b]	2100	2900	2000
1987	3047	3334	3131
1988	3101	3666	2945

[a] In 1981 South Fork Shoshone (Hunt areas 57, 58, 59, and 60S) was changed and expanded to Carter Mountain (hunt areas 58, 59, 60S, and 61). North Fork Shoshone was expanded to includes hunt areas 55, 56, 57, and 60N.

b No winter postseason population estimates were specifically given for 1986. Values listed are estimated from figures.

Table 23. Population estimates for 3 mule deer herds in District II, Wyoming east of Yellowstone National Park, 1980-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd Unit	Hunt areas	Year	Population estimate
Clarks Fork	105-109	1980	3000
		1981	1900
		1982	5000
		1983	3000
		1984	4000
		1985	3200
		1986[a]	3900
		1987	4000
		1988	6699
North Fork Shoshone	110,111,115N	1980	950
		1981	1200
		1982	2675
		1983	1200
		1984	1400
		1985	1500
		1986[a]	1600
		1987	2500
		1988	2500
South Fork Shoshone	112-114, 115S	1980	4125
		1981	3600
		1982	6150
		1983	3600
		1984	4800
		1985	3800
		1986[a]	4300
		1987	4312
		1988	4800

[a] Estimated from graph.

Table 24. Postseason population classifications for mule deer from 3 herd units in Wyoming, District II, east of Yellowstone National Park, 1980-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd	Hunt area	Year	Fawns/ 100 Does	Bucks/ 100 Does[a]	Yling. Bucks/ 100 Does	Number Classified
Clarks Fork	105-109	1980	77	16	0	219
		1981	74	14	1	734
		1982	63	12	0	495
		1983	62	11	0	582
		1984	60	17	7	1048
		1985	69	16	7	844
		1986	56	19	10	839
		1987	73	21	9	670
		1988	56	27	16	395
North Fork Shoshone	110,111, 115N	1980[b]	---	---	---	---
		1981	81	13	0	60
		1982	63	10	6	152
		1983	61	17	17	111
		1984	77	24	0	133
		1985	55	7	4	323
		1986	63	19	1	272
		1987	100	23	3	250
		1988	56	30	10	429
South Fork Shoshone	112-115S	1980	62	14	0	1016
		1981	63	26	0	804
		1982	51	19	0	729
		1983	61	14	1	402
		1984	61	13	7	2084
		1985	58	9	5	1318
		1986	61	13	8	2745
		1987	57	14	6	1284
		1988	56	27	12	900

[a] Includes total for mature and yearling bucks.

[b] Not enough animals counted for an adequate classification.

Table 25. Ratios of fawns and bucks per 100 does in the harvest from the Clarks Fork, North Fork Shoshone, and South Fork Shoshone deer herds in District II, Wyoming east of Yellowstone National Park 1980-1989. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd	Year	Fawns/ 100 Does	Bucks/ 100 Does[a]	Total Harvest
Clarks Fork	1980	0	436	574
	1981	0	1454	637
	1982	17	1083	564
	1983	9	864	671
	1984	7	1172	550
	1985	4	258	747
	1986	7	305	498
	1987	0	211	460
	1988	7	81	383
North Fork Shoshone	1980	0	573	202
	1981	0	3225	399
	1982	0	1104	289
	1983	4	774	202
	1984	0	1557	232
	1985	0	886	217
	1986	12	408	255
	1987	0	197	217
	1988	0	105	166
South Fork Shoshone	1980	0	282	794
	1981	0	1470	879
	1982	2	572	781
	1983	7	480	816
	1984	5	483	882
	1985	6	494	960
	1986	4	444	778
	1987	16	228	694
	1988	0	79	548

[a] The yearling buck harvest was not reported from 1980-1988 but the buck/100 does ratio includes yearling and adult bucks in the harvest.

Population numbers for the Trout Peak herd have been slightly increasing since 1981 and are believed to be near 497 animals in 1988 (Hurley et al. 1989). Classification data are lacking for some years (1980-1982) and few animals were classified during other years (1984 and 1985). Lamb/100 ewes ratios have been fairly stable and averaged 38 lambs/100 ewes between 1983 and 1988 (Table 27).

Prior to 1987, the population for Wapiti Ridge was believed to be stable at approximately 875 (Table 26). After correcting errors in the model, the population was then believed to be slightly increasing and near 1,000 animals in 1988. Classification data were more complete for the Wapiti Ridge herd. Except for 1981 and 1988, lamb production was relatively constant and averaged 37 lambs/100 ewes. Low lamb survival in 1988 was attributed to the harsh winter (Hurley et al. 1989).

The Younts Peak herd was believed stable at approximately 900 animals from 1981 to 1987 (Irwin et al. 1988). This herd declined 13.5% in 1988 compared to 1987 (Table 26) and was primarily due to low lamb survival (Table 27), poor forage conditions on the winter range (Hurley et al. 1989), and possibly the more severe winter. Prior to 1988, lamb/100 ewes ratios averaged 42 lambs/100 ewes.

Table 26. Bighorn sheep population estimates for 4 herd units in District II, Wyoming east of Yellowstone National Park, 1980-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd unit	Year	Population Estimate
Clarks Fork	1980	275
	1981	500
	1982	500
	1983	500
	1984	500
	1985	500
	1986[a]	500
	1987	500
	1988	500
Trout Peak	1980	---
	1981	450
	1982	450
	1983	450
	1984	450
	1985	450
	1986	500
	1987	481
	1988	497
Wapiti Ridge	1980	300
	1981	875
	1982	875
	1983	875
	1984	875
	1985	875
	1986	1000
	1987	1050
	1988	967
Younts Peak	1980	400
	1981	900
	1982	975
	1983	900
	1984	900
	1985	900
	1986	900
	1987	891
	1988	770

[a] Population estimates in 1986 were read from a graph for all herds.

Table 27. Bighorn sheep classification data from 4 herd units in District II, Wyoming east of Yellowstone National Park, 1981-1988. Adapted from Yorgason et al. (1981-1987) and Hurley et al. (1988, 1989).

Herd unit	Year	Rams/ 100 ewes	Lambs/ 100 ewes	Total Classified
Clarks Fork	1981	66	50	13
	1982	62	33	41
	1983	16	41	19
	1984	123	33	77
	1985	---	---	---
	1986	100	50	10
	1987	---	---	---
	1988	76	45	84
Trout Peak	1981	---	---	---
	1982	---	---	---
	1983	70	33	49
	1984	20	40	16
	1985	73	45	24
	1986	50	38	94
	1987	35	37	74
	1988	55	35	203
Wapiti Ridge	1981	28	89	107
	1982	69	37	122
	1983	48	34	159
	1984	47	40	263
	1985	53	36	318
	1986	57	35	321
	1987	30	40	347
	1988	42	18	354
Younts Peak	1981	31	48	52
	1982	19	37	42
	1983	41	31	83
	1984	37	27	67
	1985	28	59	263
	1986	27	44	179
	1987	34	48	91
	1988	31	14	188

WYOMING DISTRICT I SUMMARIES

Seasonal Ranges and Distribution

Elk

Elk, south of Yellowstone National Park, occur in the Jackson and Targhee herd units. The Jackson herd primarily winters in the Gros Ventre River valley and on the National Elk Refuge. These winter ranges are 48 km-64 km (30-40 miles) south of Yellowstone National Park (Fig. 40) and distant from areas wolves would likely inhabit. Based on 97 radiocollared elk (Smith and Robbins in prep.), approximately 40% of the Jackson elk herd unit summers in Yellowstone National Park (28.2%) and the adjacent Teton Wilderness (11.8%).

Spring migration lasted 21 days for elk migrating to Yellowstone National Park. Many cows calved enroute to summer ranges and mean period of stay on summer ranges in the park was 160 days (Smith and Robbins in prep.). October snows precipitated an earlier fall migration but did not necessarily result in an earlier arrival at the National Elk Refuge. Mean fall migration lasted 19 days.

The Targhee herd unit summers in Wyoming (Fig. 40). In winter, these elk migrate west onto winter ranges in Idaho or to south exposures of several drainages within about 10 km (6 miles) of the Idaho-Wyoming stateline (Lockman et al. 1989).

Mule Deer

Mule deer from the Jackson herd unit winter near the town of Jackson, 64 km-80 km (40-50 miles) from Yellowstone National Park (Fig. 41), well away from areas wolves would likely occupy. Summer migrations into Yellowstone are highly likely (Lockman et al. 1989).

Mule deer from the Targhee herd unit winter in Idaho (84% were seen in Idaho) or in Wyoming straddling the stateline in the Victor, Fox, Kiln, Teton, South Badger, and South Leigh Creeks (Lockman et al. 1989, Fig. 41). Some of these deer undoubtedly summer in or near Yellowstone National Park.

Moose

Moose range south of Yellowstone National Park in the Jackson and Targhee herd units. Tagging and neckbanding studies conducted in the late 1960s and early 1970s (Houston 1968, Lockman et al. 1989) suggest moose that winter along the Buffalo River summer in Yellowstone and Grand Teton National Parks, the Teton Wilderness, and in upper Spread Creek (Fig. 42).

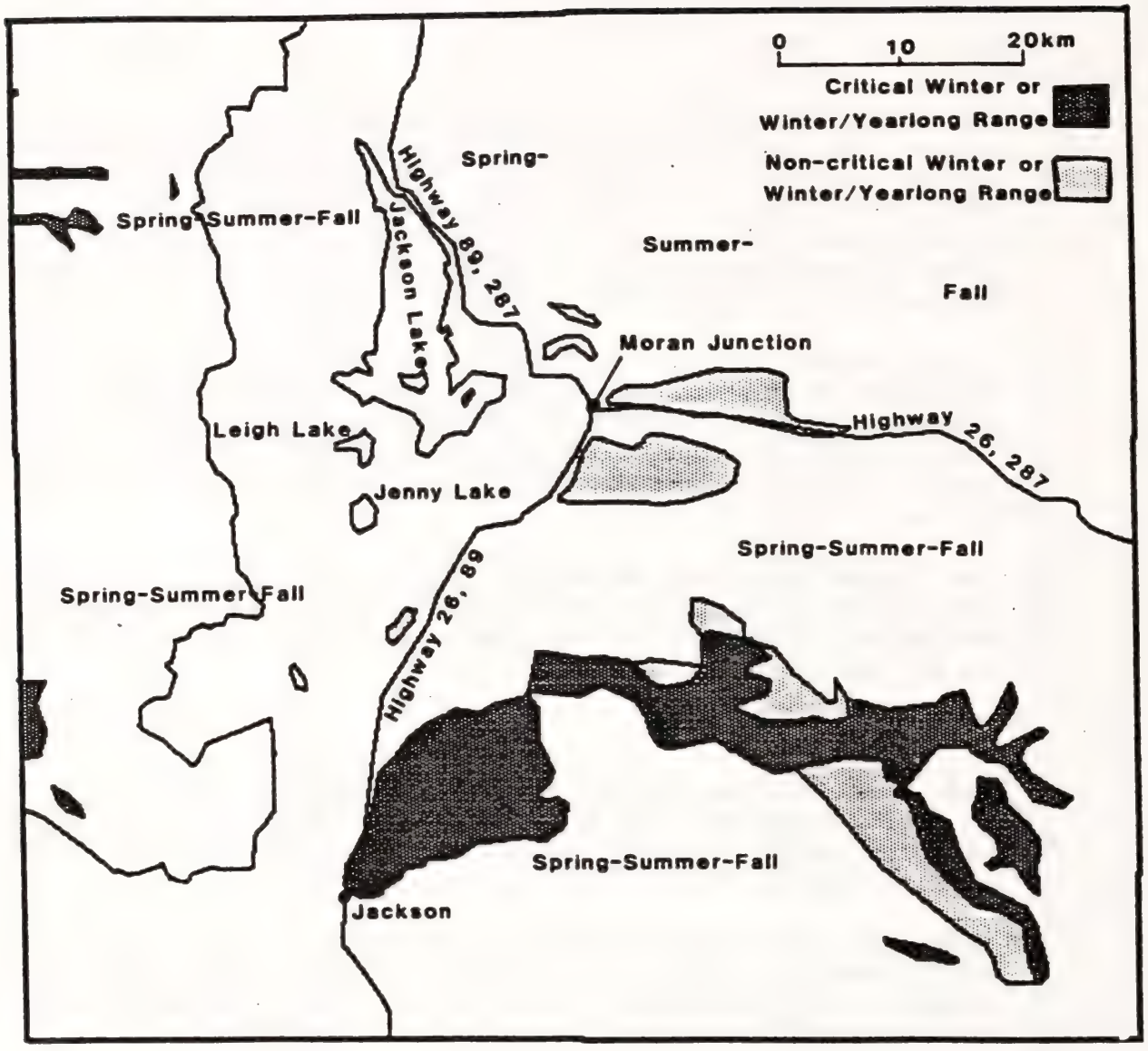


Fig. 40. Spring-winter-fall, and winter ranges for the Jackson and Targhee elk herds in District I in Wyoming south of Yellowstone National Park. Seasonal ranges adapted from Lockman et al. (1989).

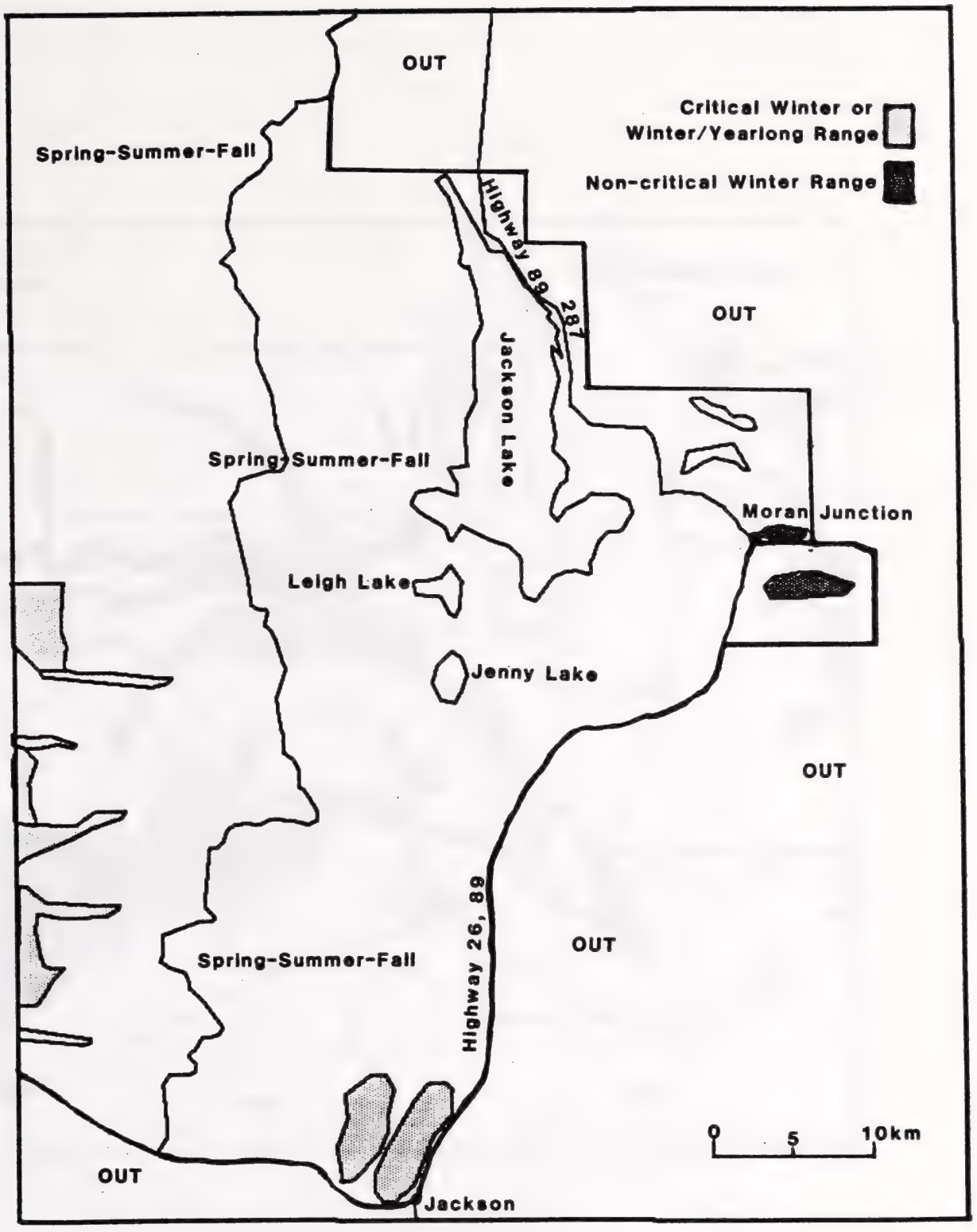


Fig. 41. Spring-summer-fall, and winter ranges for the Jackson and Targhee mule deer herds in District I in Wyoming south of Yellowstone Park. Seasonal ranges adapted from Lockman et al. (1989).

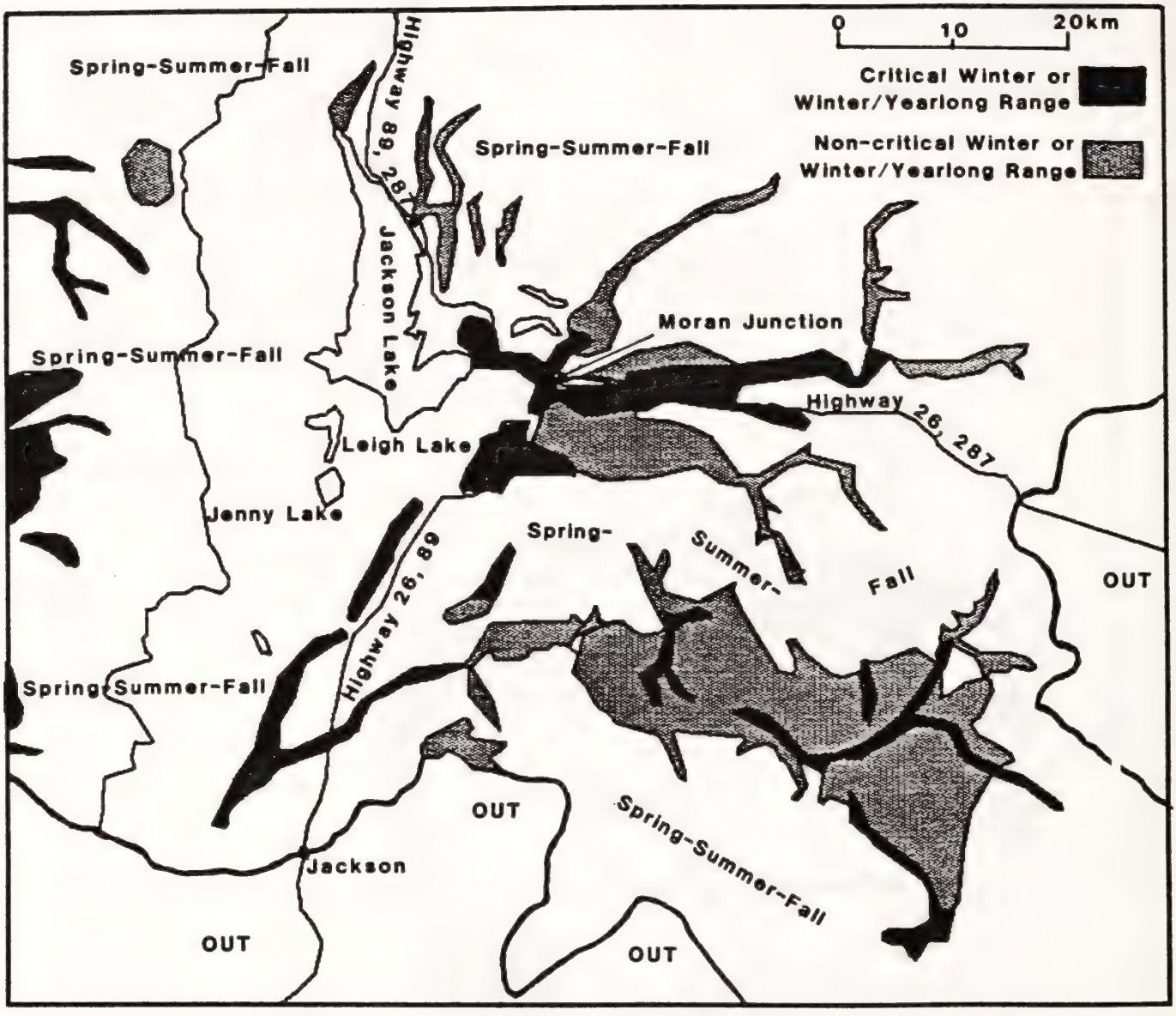


Fig. 42. Spring-summer-fall, and winter ranges for the Jackson and Targhee moose herds in District I in Wyoming south of Yellowstone Park. Seasonal ranges adapted from Lockman et al. (1989).

SECTION 3

Computer Simulation Models

WOLF RECOVERY FOR YELLOWSTONE NATIONAL PARK:

A SIMULATION MODEL

Mark S. Boyce
University of Wyoming
Department of Zoology and Physiology
Laramie, WY 82071

WOLF RECOVERY FOR YELLOWSTONE NATIONAL PARK: A Simulation Model

Mark S. Boyce, University of Wyoming, Department of Zoology and Physiology, Laramie, WY 82071

EXECUTIVE SUMMARY

A stochastic simulation model of gray wolf (Canis lupus) recovery for Yellowstone National Park was developed based upon existing data on wintering ungulates in the park and extrapolations from observations of wolf predation in other areas. The following conclusions may be reached based upon the behavior of this computer model:

1. Consummation of wolf recovery will depend in part on the number of wolves released in the park. There is a moderately high probability of extinction for the initial inoculum if fewer than ten wolves are released. Approximately 30 wolves should be released if assurance of wolf recovery is desired.

2. There is no combination of management choices where wolf predation has devastating consequences to elk (Cervus elaphus) populations in the park. The reason is that social behavior limits wolf densities so that the wolf population cannot attain total numbers high enough to depopulate the elk herd.

3. Wolf predation will cause a reduction in the number of bison (Bison bison), elk, moose (Alces alces), and mule deer (Odocoileus hemionus) in the park. Mean elk numbers may be expected to be 15%-25% lower if wolf recovery is accomplished. The effect of wolves on bison numbers will be less, with a reduction of only 5%-15%. Moose numbers on Yellowstone's northern range may decline if heavy hunter harvest is sustained in Montana. Mule deer may be locally susceptible to wolf predation, but the population is secure from extirpation because wintering areas exist where it is unlikely that they will suffer predation by wolves. It is assumed that wolves will have minor consequences to other vertebrates including bighorn sheep (Ovis canadensis) and pronghorn (Antilocapra americana).

4. Wolf recovery in Yellowstone National Park is not contingent upon discontinuing elk hunting north of the park in Montana. However, continued hunting when combined with wolf recovery will result in smaller ungulate populations in the park. Termination of elk hunting after wolf recovery could increase the number of elk wintering in the park by 5%-15%, while reducing variation in elk numbers by 20%-30%.

5. Ungulate numbers in Yellowstone National Park undergo substantial fluctuations due to climatic variation. The variance in ungulate numbers is predicted to decrease subsequent to wolf recovery, i.e., wolves will have a stabilizing effect on ungulate population size.

6. If the recovery zone includes additional public lands surrounding Yellowstone National Park, there is a substantially higher probability that wolf recovery can be accomplished. This additional land will increase the total number of possible wolf territories in the greater Yellowstone ecosystem and thereby reduce the probability of extinction for the introduced wolf population.

7. Wolf numbers are expected to fluctuate substantially, but they should eventually reach 50-120 animals under most management scenarios. If wolves are culled at 40% or more, there is a high probability that the wolf population will be extirpated. Once established, it is expected that 15-25 wolves may leave the park each year.

8. It is impossible to precisely predict the consequences of wolf recovery in the greater Yellowstone ecosystem because vagaries of climate can have enormous consequences to any ecological process. Any realistic model of wolf recovery must be stochastic, i.e., include random variation in certain ecological variables.

9. To refine predictions of the model, research is required to obtain detailed information on plant-herbivore dynamics, on moose and deer population dynamics in the park, and on the functional response of wolf predation. Implementation of wolf recovery should be accompanied by a carefully-designed monitoring program to test predictions of this model.

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WOLF RECOVERY FOR YELLOWSTONE NATIONAL PARK: A Simulation Model

Mark S. Boyce, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071

ABSTRACT: A stochastic predator-prey model was developed to simulate the probable consequences of gray wolf (Canis lupus) recovery in Yellowstone National Park. Abundant prey in the park enhances the probability that wolf recovery can be accomplished. Wolves are expected to reduce prey abundance by 10%-30%, with elk (Cervus elaphus) as the principal prey species. Predation by wolves will dampen the substantial fluctuations that park ungulates undergo attributable to variations in climate. The consequences of wolf recovery to native ungulates will depend upon management practices. Culling wolves that leave the park and poaching within the park reduces the total number of wolves occupying the park, increases the risk of extinction for the wolf population, and increases the number of ungulates. Increasing the area included within the recovery zone will reduce the probability that wolves will go extinct during the century following reintroduction.

Hunting of ungulates outside of the park boundaries is compatible with wolf recovery in the park. This is possible because there is no hunting within the park, culling rates outside the park are not high, and compensatory mortality and natality permit moderate levels of hunting as well as predation.

The "WOLF" program is very "user friendly" to encourage interactive use by individuals unfamiliar with computers.

INTRODUCTION

The gray wolf (Canis lupus) was extirpated from Yellowstone National Park by U.S. government trappers between 1914 and 1926. Since then, occasional reports of wolves in Yellowstone National Park have been recorded (Weaver 1978), but no recent records exist of wolves breeding in the park. In recent years, public attitudes towards predators have changed; predators are more commonly viewed as an integral component of natural ecosystems (Mech 1970, Despain et al. 1986, Dunlap 1988). An increasing proportion of the American public desires that wolves be reestablished in Yellowstone National Park (McNaught 1987, Bath 1990).

In 1987, the U.S. Fish and Wildlife Service approved a recovery plan for the gray wolf (U.S. Fish & Wildlife Service 1987). In 1988, Congress appropriated $200,000 for wolf studies by the U.S. Fish and Wildlife Service and the National Park Service. This model is a result of the Congressional mandate to conduct research to determine the probable outcome from wolf recovery.

The purpose of this simulation model is to predict the probable consequences of wolf reintroduction on ungulate populations in Yellowstone National Park. Since we cannot be certain of future management activities, the model allows the user to choose several likely management scenarios. By manipulating such alternatives, the user of the model can explore the consequences of management actions. In particular, it is essential to be able to anticipate if wolves will be culled if they leave the park, if poaching can be controlled within the park, and if hunting for bison (Bison bison) and elk (Cervus elaphus) will continue in Paradise Valley, north of the park.

Any such model must incorporate the natural variability in the environment, because the vagaries of climate can have enormous consequences to any ecological process. Therefore, the model is a stochastic one, i.e., it contains random variation in climatic variables. Such stochastic model structure is important because it helps to educate the user that it is impossible to predict precisely the consequences of wolf recovery.

It is not the purpose of this modeling effort to offer recommendations for whether wolf recovery should take place, but rather to provide resource managers with an additional tool to assist them with the wolf recovery decision.

According to Kellert (1980, 1986) and Noss (1989), education is probably the most significant contributor to positive attitudes towards wildlife. For this model, it is apparent that public education is an important future use. There exist numerous scientific investigations of predator-prey relationships, but the principles underlying this body of scientific knowledge are not widely known by the American public. If this model is to be used by its intended audience, it is essential that it be simple, "user friendly," so that it is accessible to the maximum number of people. The model will be used as a tool for educating students, park rangers, resource managers, politicians, as well as the general public.

METHODS

A dynamical systems model composed of stochastic difference equations where certain parameters are input directly or indirectly by the user was developed. This model is used to project time series of wolf and ungulate populations for 100 years into the future. The core model is programmed in Turbo Pascal and the program has been entitled "WOLF." To run the model requires less than 96 kilobytes of RAM, and screen drivers have been included so that the model should run on any IBM PC or AT compatible computer in 8086-, 80286-, or 80386-based machines having graphics capability. The program was tested on over 20 different microcomputer configurations and was compatible with each. Disks are available in both 5-1/4 inch and 3-1/2 inch disk formats, and none of the software is copy protected. Users are welcome to copy and distribute the program without permission.

A priority in the development of the model was that it be interactive. The closest approximation to reality for populations in a seasonal environment is a system of differential equations with seasonality imposed by continuous-time oscillations, i.e., sinusoidal forcing functions (Boyce and Daley 1980). However, such models require considerable computation time that would render them ineffective for interactive use. Thus, difference equations were employed. The model was stable in deterministic runs, which suggests that the discrete time simplification did not substantially complicate the behavior of the model.

Additionally, the age structure was collapsed so that the program would run in a reasonable length of time. Although predation mortality may vary among ages, this has the consequence of scaling predation rates. A Lefkovitch (1965) nonsenescent age-structured matrix incorporated into the same model produced only minor effects on the projected population behavior.

Ungulate Population Dynamics

There are six ungulate species in Yellowstone National Park that will be prey for wolves (Houston 1982, Despain et al. 1986). In the order of their population biomass, these species are elk, bison, mule deer (Odocoileus hemionus), moose (Alces alces), bighorn sheep (Ovis canadensis), and pronghorn (Antilocapra americana). In addition, there are occasional white-tailed deer (Odocoileus virgianus), mountain goats (Oreamnos americana), and several species of small mammals and birds that may form a portion of the diet of wolves, but it is not anticipated that these will be major prey items (Singer 1990). Beavers (Castor canadensis) are important summer prey for wolves in Alaska (Boyce 1974), Minnesota (Frenzel 1974, Van Ballenberghe et al. 1975, Fritts and Mech 1981, Fuller 1989), Isle Royale (Peterson 1977), Ontario (Theberge and Strickland 1978, Voigt et al. 1978), and Manitoba (Chadwick 1987), but beavers are not abundant enough in Yellowstone to be significan prey for wolves.

Investigations by Houston (1982), Merrill et al. (1988), and Merrill and Boyce (1990) provide background information on the dynamics of elk and bison in Yellowstone National Park which forms the structural basis for ungulate population dynamics in the "WOLF" program. The elk is far and away the most abundant ungulate species in the park, and therefore, a clear picture of the population dynamics of elk is critical for any model of wolf recovery in Yellowstone.

Survival and fecundity for both elk and bison are density dependent (Fowler and Barmore 1979). In addition, summer forage production has significant influences on population dynamics for each of these species (Merrill et al. 1988, Merrill and Boyce 1990), and severe winter weather can result in high mortality (Houston 1982). Survival of elk calves is a function of both winter climate and population density (Sauer and Boyce 1979, 1983; Boyce 1989).

Following Houston (1982), Picton (1984), and Merrill and Boyce (1990), a modified Lamb's Index for winter severity was calculated from temperature and precipitation measurements for December through March at Mammoth Hot Springs, Wyoming. When both temperature and precipitation are average, Lamb's Index is zero. Integer additions or subtractions to the Lamb's Index are made for each standard deviation from the average that occurs for temperature and precipitation. Increased precipitation contributes positively to winter severity whereas increased temperature has a negative effect on Lamb's Index for winter severity.

Mean and variance of green herbaceous phytomass (kg/ha) was estimated annually for the period 1971-1988 from LANDSAT imagery and related to elk and bison per capita population growth rates (Merrill et al. 1988). High quality summer forage can increase reproduction by enhancing the condition of the dam, and also favors rapid growth and subsequent survival of calves (Merrill and Boyce 1990).

The influence of winter severity and summer range production on per capita growth rates was estimated using multiple linear regression. Here the per capita population growth rate, r(t) is defined:

$$r(t) = \ln\{[N(t+1) + H(t+1)]/[N(t) - LGH(t)]\} \qquad \text{(equation 1)}$$

where N(t) is the winter population count minus adult males in year t, LGH(t) is kill of elk during the late Gardiner hunt (Unit 313) in year t, and H(t+1) is the harvest from Unit 316 in Montana during year t+1. The following model was fitted using least squares procedures:

$$r(t) = r_o - b_1 N(t) + b_2 L(t) + b_3 P(t) \qquad \text{(equation 2)}$$

with the equation defined as follows: b_is are the regression coefficients r_o is the potential population growth rate, L(t) is Lamb's Index for winter severity, and P(t) is green herbaceous phytomass during summer.

This regression model can be rewritten as a difference equation for predicting the dynamics of elk populations:

$$N(t+1) = N(t)\exp[r_o - b_1 N(t) + b_2 L(t) + b_3 P(t)] \qquad \text{(equation 3)}$$

where L(t) and P(t) are independent random normal variables. By using mean values of climate and herbaceous phytomass, this model collapses to a difference equation approximation of the logistic model with N(t) ultimately converging on carrying capacity, K, where r(t) = 0. By setting $\ln[N(t+1)/N(t)] = 0$ in equation 3, we can solve for $K = r_o/b_1$.

For elk, fitting data to equation 2 accounted for over 88% of the variance in per capita growth rates ($P < 0.001$). An estimate for r_o was based upon Eberhardt's (1987) analysis of the northern Yellowstone elk herd. The observed winter census of elk on the northern Yellowstone elk winter range is plotted

with a logistic fit to the data (Fig. 1). Similarly, the proportion of cow elk with calves at heel was correlated with green herbaceous phytomass and population size. To apply this model of elk population dynamics to the entire park, the carrying capacity for elk was increased above the estimates for the northern range to include elk wintering in other portions of the park (Cole 1983, Boyce 1989, Singer 1990).

The model fitted for bison was similar to that for elk (Merrill et al. 1988). For both species, a linear model fit r(t) as a function of N(t) better than a convex one, despite the usual tendency for vertebrates to have concave density dependence (Fowler 1987, Boyce 1989). Frances Cassirer (Univ. of Idaho pers. comm.) suggested to me that this may be a consequence of recent range expansion by both bison (Meagher 1989a, 1989b) and elk (Houston 1982) on the northern range, which would tend to flatten the density-dependent function.

A detailed model for moose and deer is not described because empirical data are inadequate. Carrying capacity is estimated for moose and deer based upon approximations of population size in recent years, and r_o is estimated for these species from literature reports (Wallmo 1981). A value of r_o for moose was reduced to 0.2 due to heavy hunting pressure outside the park (Singer 1990).

Bighorn sheep and pronghorn were not included in the simulation model. Both of these prey species occur at low numbers in Yellowstone National Park and their influence on wolf population dynamics would therefore be negligible. Bighorn sheep are not expected to be influenced by wolf recovery because they largely avoid wolf predation by staying near escape terrain (Cowan 1947, Murray 1987). Pronghorn are not likely to suffer heavy wolf predation either because they winter near the town of Gardiner, Montana, where human occupation may deter wolves from being present.

Stochastic Variation

At our current state of understanding, it is not possible to predict climatic variation among years. We will presume, therefore, that climatic variation is stochastic with mean and variance comparable to that which has occurred during the past 50 years. For example, this results in a Lamb's Index with an average of zero and a standard deviation of 6.5.

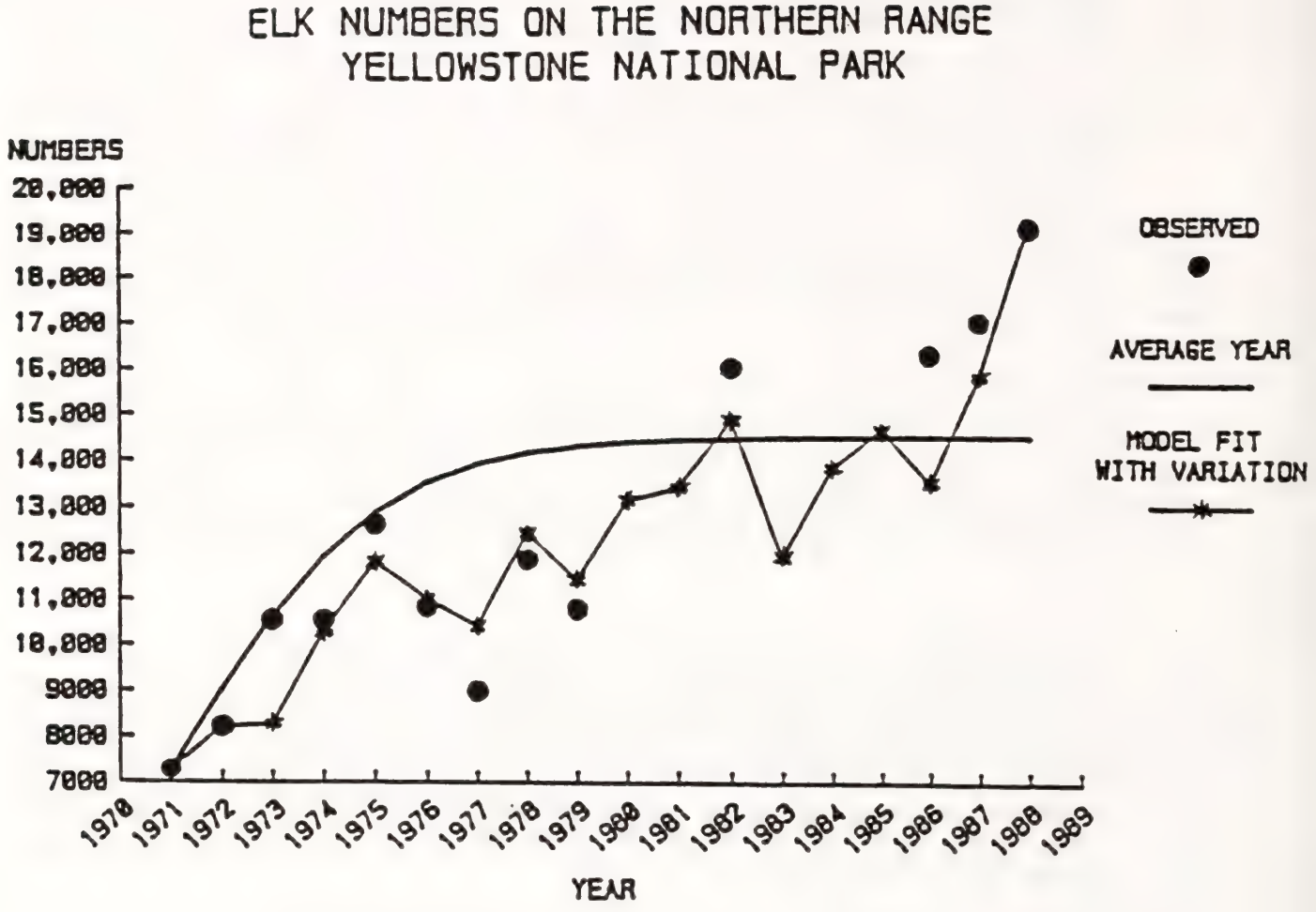

Fig. 1. Observed winter census of elk in Yellowstone National Park plotted with a logistic fit to the data (solid line). Asterisks indicate the counts predicted from equation 3 using observed values of winter severity and summer phytomass.

To create normally-distributed random variables, a (0,1) random number generator, RAN(i), was employed. These evenly distributed random numbers are transformed into normally-distributed random numbers, RANDNORM(t), by:

$$RANDNORM(t) = \sum_{} RAN(i) - 6 \qquad \text{(equation 4)}$$

with mean = 0 and standard deviation = 1. This distribution can be adjusted by linear transformation:

$$X(t) = s * RANDNORM(t) + u \qquad \text{(equation 5)}$$

where X(t) is a normally-distributed random variable with mean, u, and standard deviation, s.

The 1988 Fires

Ungulate population dynamics are expected to be affected by the extensive fires of 1988, and generally the ungulates included in the "WOLF" program are known to increase in postfire habitats (Boyce and Merrill 1990). To incorporate the effects of the 1988 fires, a literature review formed the basis for a maxim function simulating range improvements for both elk and bison in the park (Boyce and Merrill 1990). For elk, the carrying capacity in year, t, is assumed to follow the following maxim function:

$$K_{elk}(t) = 168\ t \exp(-0.2t) \qquad \text{(equation 6)}$$

and similarly for bison:

$$K_{bison}(t) = 253\ t \exp(-0.3t) \qquad \text{(equation 7)}$$

Detailed justification for these functions is provided by Boyce and Merril (1990).

Predation

Only predation by wolves is incorporated into the "WOLF" program, although other predators of ungulates occur in Yellowstone National Park, including coyotes (Canis latrans), cougars (Felis concolor), black bears (Ursus americanus), and grizzly bears (Ursus arctos). Bears can occasionally be significant predators on elk (Schlegel 1988, Singer and Harting 1988) and other ungulates (Singer 1987). Bear predation is not explicitly incorporated into these simulations, although it is assumed to be a component in the past performance of ungulate populations.

Wolf Life History

The gray wolf is the largest species of wild canid, with males occasionally exceeding 50 kg (Mech 1974). The species historically occupied much of North

America but is now substantially restricted in distribution. Sizable populations still exist in Canada and Alaska, and recently wolves have appeared in Glacier National Park, Montana, but the only truly viable population in the contiguous 48 states occurs in northern Minnesota (Mech 1970, 1974).

Several wolf den sites were recorded in northern portions of Yellowstone prior to the species extirpation. The average litter size for wolves in Yellowstone National Park was 7.8, ranging from five to 14 pups (N = 10) (Weaver 1978). Sexual maturity may occur at two years, although most wolves do not breed until age three (Mech 1974) and sometimes not until age four. The age at first breeding may vary with the maturity and density of the wolf population. Reproductive rates for wolves in Alaska average one pup per wolf per year (Chapman 1977). Most packs only produce one litter per year, but, when food is abundant, it has been observed in Alaska that 15%-20% of the packs may bear two litters, i.e., there will be two breeding females in a pack (Haber 1977, Ballard et al. 1987).

Social behavior of wolves imposes density dependence which can influence the upper limit to population density. In undisturbed populations, approximately 60% of the mature females breed, whereas upwards of 90% may breed in populations heavily exploited by man (Rausch 1967, Pimlott et al. 1969) or in rapidly increasing populations (Fritts and Mech 1981). Clearly, density dependence is an essential component of any realistic model of wolf population dynamics (Packard et al. 1983).

Pack size in Yellowstone National Park is assumed to be seven or eight wolves. However, a high rate of dispersal and reproduction at minimum age may result in smaller mean pack size for several years during wolf establishment (Fritts and Mech 1981:25-26). Kill rates are lower for small wolf packs (Van Ballenberghe 1987). Furthermore, kill rate per wolf tends to decline as pack size increases, and pack size has been observed to be larger where little human exploitation of wolves occurs (Peterson et al. 1984), as would probably be the case within Yellowstone National Park. These effects related to pack size variation have not been incorporated into the model.

For estimating maximum wolf pack densities, it is assumed that there will be no interstitial spaces between packs when population density is high (Messier 1985, Ballard et al. 1987). Wolf territories may be larger and packs smaller during the colonizing phase of wolf recovery than after large numbers of wolves have been established (Ream et al. 1990). During winter, all wolf packs are expected to be restricted to ungulate winter range areas in the park. The principal winter range in Yellowstone National Park is the 830 km^2 northern range (Houston 1979). There may also be adequate numbers of ungulates to support wolves in the Madison-Firehole area (Cole 1983), and perhaps along the upper Yellowstone River south of Yellowstone Lake (Boyce 1989).

Winter food requirements for wolves are approximately 3.2 kg da^{-1}; 3.6 kg da^{-1} are required for successful reproduction (Mech 1977, Weaver 1979). Information

on the density of elk necessary to sustain wolves was unavailable, although Messier (1985) found that moose densities lower than 0.2 moose/km^2 were inadequate to support wolves. During winter, large portions of the interior of Yellowstone National Park are virtually devoid of ungulates and, therefore, could not support wolves.

Functional Response

Key structural features of any predator-prey model are functional and numerical responses. The functional response is characterized by an equation which governs the per capita rate at which prey are captured as a function of the number of prey available to the predators. For mammals, functional responses are usually logistic (S-shaped), often labelled a Type III functional response (Holling 1959). Mathematically, the form of such a functional response is:

$$F_i = C_i * N_i^2 / (1 + [C_i (1/F_{max}) N_i^2] \qquad \text{(equation 8)}$$

where F_i is the number of the ith prey species taken per predator per unit time; C_i is a scaling constant; N_i is the number of ungulates, and F_{max} is the asymptotic maximum number of prey killed per predator for large populations of prey.

In Table 1, all of the population and functional response parameters for each of the four species of ungulates modeled in the "WOLF" program have been summarized. Note that the carrying capacities for ungulates are equilibrium population levels which would eventually be attained in the absence of wolves. The carrying capacity for each of the ungulate species tracks the responses to fire as derived from equations six and seven.

Average kill rates vary depending upon the species and density of prey. Mech and Frenzel (1971) reported an average kill rate of one deer per 18 days (2.5 kg wolf^{-1} da^{-1}), whereas on Isle Royale, Michigan, Mech (1966) observed that one moose was killed per 45 days (6.3 kg wolf^{-1} da^{-1}). This value is remarkably close to Keith's (1983) review of the results of five North American studies in which he calculated one moose killed per 41 days. The highest kill rate observed was one moose/1.8 days for a pack of 8-10 wolves during a 35-day period (Peterson 1977). This would yield a F_{max} of 22.5 moose per year, but it is unlikely that wolves could sustain such a high kill rate through an entire year.

In Banff and Jasper Parks, midwinter consumption rates of elk were estimated to range between 0.14 and 0.2 kg per kg of wolf per day (Weaver 1979). In Riding Mountain National Park, Manitoba, where wolves were feeding extensively on elk, Carbyn (1983) found daily consumption by wolves to average 0.21 kg of prey per kg of wolf biomass. If wolf mass averages 40 kg, this yields approximately 8.4 kg wolf^{-1} da^{-1}, or the equivalent of about 14 elk wolf^{-1} yr^{-1}.

Table 1. Population, functional response, and numerical response coefficients for each of the four ungulate species modeled in the "WOLF" program.

Species	r_o	r_o/K	W	P	F	F_{max}	R
Elk	0.43	2.7×10^{-5}	0.0233	0.00036	2.0×10^{-7}	25	0.075
Bison	0.23	9.2×10^{-5}	0.0079	0.0002	1.5×10^{-7}	10	0.13
Moose	0.2	2.5×10^{-4}	0.01	0.0001	1.5×10^{-7}	20	0.09
Deer	0.4	1.3×10^{-4}	0.009	0.0003	2.5×10^{-7}	110	0.015

r_o = potential per capita population growth rate.

K = winter carrying capacity for Yellowstone.

W = coefficient scaling the response to winter severity.

P = response to green herbaceous phytomass.

F = functional response coefficient, scaled to preference.

F_{max} = maximum number of prey killed given unlimited prey abundance--usually determined by satiation.

R = numerical response coefficient, scaled to the body mass of each prey species.

Wolves prefer elk as prey over moose, and elk are killed at one-third higher incidence relative to their abundance (Carbyn 1983), probably because elk are more vulnerable than moose. Even small wolf packs have been observed to kill elk (Carbyn 1983), whereas moose are often tested multiple times before one is attacked (Mech 1966, 1970).

Maximum per capita kill rates for elk are estimated to be 25 elk per annum which forms the upper asymptote of the functional response curve (Fig. 2). This is higher than typical maximum consumption rates for wolves, presuming that some surplus killing will occur when prey are exceptionally abundant. Because elk are expected to always be more abundant than other ungulates, they will dominate wolf diets. Therefore, no switching by wolves is anticipated to occur amongst the four main ungulate prey species available in Yellowstone National Park.

For functional response estimation, it is assumed that bison are more difficult prey for wolves to kill than are elk. Yet, in northern Canada, it has been demonstrated that wolves can effectively predate and subsist on bison, the

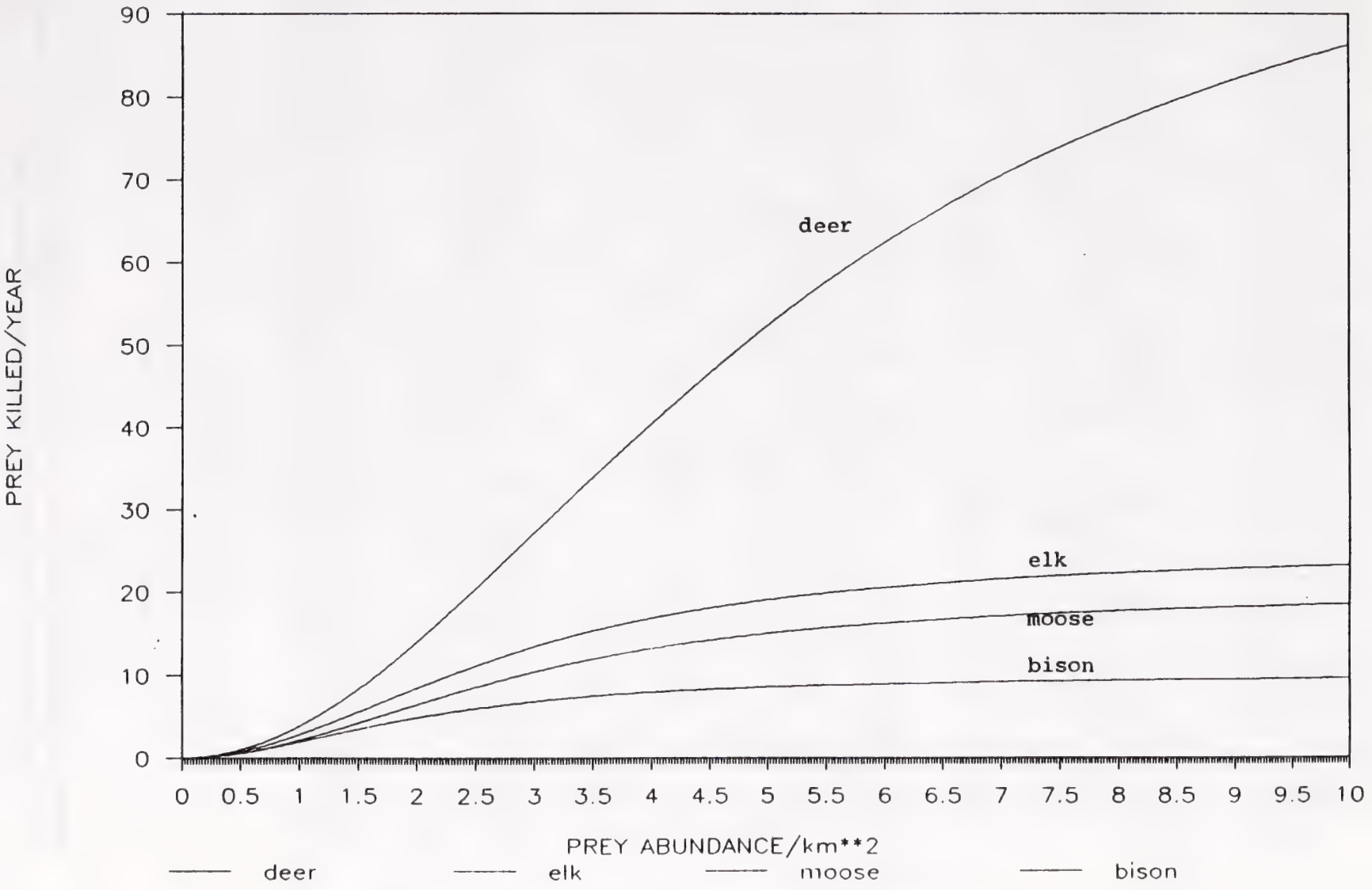

Fig. 2. Functional response curves for four species of ungulates.

largest of North American land mammals (Carbyn and Trottier 1987). The most susceptible are yearling bison that are no longer under the defense of their dams, although in one study proportionately more bulls were taken by wolves (Oosenbrug and Carbyn 1983). Bison may actually be slightly easier prey for wolves than are moose, especially in snow where moose can maneuver better with their long legs (Telfer and Kelsall 1984). For the "WOLF" program, preference for bison is scaled at 67% of that for elk, but, because they average more than twice as large as elk, the maximum possible kill rate under high densities (F_{max}) is ten bison per wolf per year (Table 1).

Data on moose and deer in Yellowstone National Park are meager relative to that available for elk and bison. Therefore, many of the parameters are based upon literature survey. Indeed, there has probably been more research on wolf predation on moose than on other ungulates (Mech 1966, Crete et al. 1981, Gasaway et al. 1983, Ballard et al. 1987). Based upon the Canadian studies of Carbyn (1974, 1983), a preference for moose that is 0.67 that of elk and deer has been assigned. Because the Shiras moose is slightly larger than elk in Yellowstone National Park, a F_{max} 0 20 is assumed.

Deer are assumed to be 1.3 times as preferred as elk (Cowan 1947); however, many more elk winter in the park than deer. When scaled for their smaller body size, a F_{max} of 110 deer killed per wolf per annum when deer are extremely abundant was estimated. At densities observed on the northern range, we can expect an average of less than 2.5 deer killed per wolf per year averaged over all wolves in the park. On the northern range, approximately 700-1,000 mule deer winter in the vicinity of Gardiner, Montana, thereby creating a refuge from winter predation by wolves. This refuge was modeled as a step function whereby wolf predation cannot reduce the deer population below 700 animals.

Numerical Response

The numerical response, as opposed to the functional response, describes the rate at which captured prey are converted into predator offspring. Again this is a logistic function for mammalian predators and is assumed to be a multiple of the functional response of equation 8.

For wolf population growth, a multiple-species numerical response function is used, where $N_{wolf}(t+1)$ is the number of wolves in year, t+1, which is a function of the abundance of each prey species and the number of wolves at time, t:

$$N_{wolf}(t+1) = N_{wolf}(t)\exp\{[0.075\ F_{elk}(t) + 0.13\ F_{bison}(t) + 0.09\ F_{moose}(t) + 0.015\ F_{deer}(t)] - (r/K_{wolf})\ N_{wolf}(t) - 0.68\} \qquad \text{(equation 9)}$$

where the coefficients before the F_is are scaled proportionately to the mean biomass for each prey species (elsewhere these coefficients are labeled R_is).

The portion of equation 9 within square brackets represents the numerical response. The constant, r, in the density-dependent term is assumed to be 0.8.

K_{wolf} is the carrying capacity for wolves determined by territoriality, which in turn is a function of the prey base available to wolves in Yellowstone National Park. Territory size for Yellowstone is estimated based upon Walters et al.'s (1981) review of the effect of prey biomass on wolf territory size. Minimum territory size for packs will be 130 km^2. Even for resident wolves, it is assumed that territories may be as much as 50% outside the "maximum compression elk winter range" outlined by Houston (1982). In most years, considerably more area than the "maximum compression elk winter range" will be part of the winter range for ungulates. On average, it is assumed that each pack might occupy 65 km^2 of the 830 km^2 on the northern range, setting a K_{wolf} on the northern range of approximately 12 packs.

When all species of prey are at population sizes near their respective carrying capacities and N_{wolf} is near zero, the wolf population will attain a maximum population growth rate comparable to the r_o term for ungulates (Equation 8). For wolves, litter sizes are large and consequently potential population growth rates can be higher than for ungulates. Ballard et al. (1987) observed a finite growth rate of 2.4 in Alaska, although this was very likely due in part to immigration into the area. For the "WOLF" program, wolves have a potential growth rate of 1.8. This means that during the initial growth phase, the wolf population could attain an annual increase of 80% per year once a stable age distribution is reached.

Currently, there is debate about the mechanisms that create logistic-shaped functional and numerical response functions (Caro 1989). The logistic shape has been verified empirically and the concavity of the right-hand side of the curve (Fig. 3) is generally agreed to be a consequence of predator satiation (Holling 1959, Taylor 1984). The debate concerns the convex portion of the curve where prey densities are less than at the inflection point at $F_{max}/2$. Traditionally it has been claimed that the convex portion of the curve is a consequence of the predator developing a search image. For example, wolves actually might locate prey more accurately at the expense of detecting other prey items (Krebs 1971). But it also seems quite likely that it results from learning where to hunt, learning how to handle a new prey species better, learning to accept unfamiliar prey, or learning to adjust search rate (Allen 1989, Caro 1989). For purposes of this modeling effort, however, the mechanisms do not matter as long as the shape of the functional and numerical response curves is appropriate.

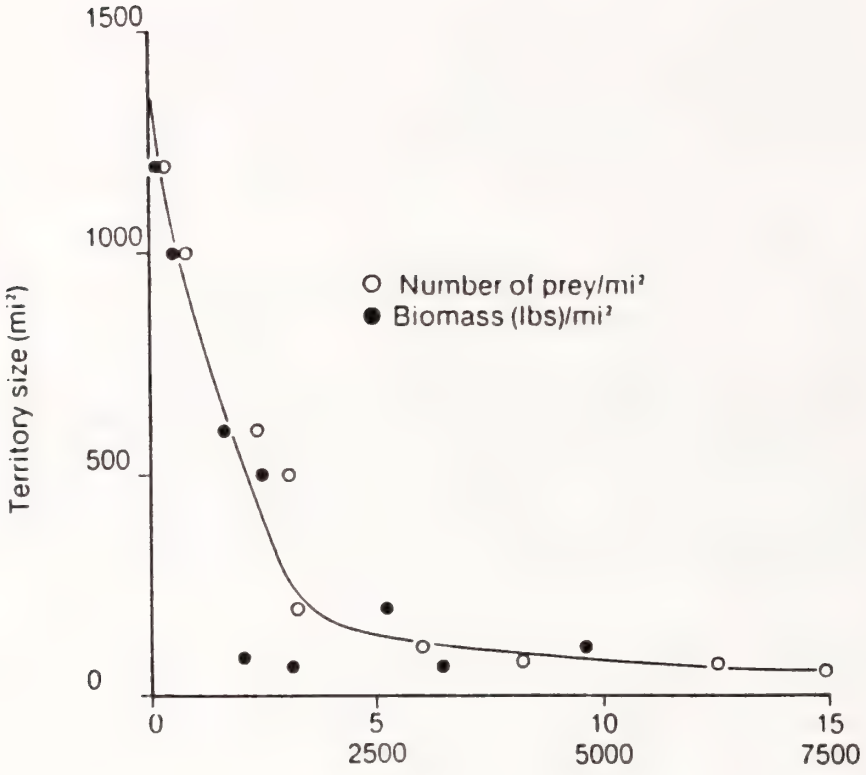

Fig. 3. Wolf territory size as a function of prey biomass.

Surplus killing by wolves is known to occur, particularly of young prey or other individuals that are vulnerable (Eide and Ballard 1982, Miller et al. 1985). Carbyn (1983) documented that wolves killed elk in excess of their food requirements in late winter, because wolves have improved mobility on crusted snow, and elk are in weaker condition at the end of the winter. It might be suggested that surplus killing by wolves would be heaviest in years with a high Lamb's Index, although wolves have a difficult time maneuvering through deep powdery snow. It might also be speculated that high prey density years may be years when surplus killing would be more prevalent. Yet, in northwestern Minnesota, two-thirds of the deer taken by wolves were in low density deer areas, apparently where deer were more vulnerable (Fritts and Mech 1981).

To anticipate surplus killing by wolves in this draft of the "WOLF" program, the maximum potential kill rates in the functional responses for each ungulate species have been increased (Equation 8, Table 1). This might also be interpreted as prey "wastage" of approximately 10% when prey are exceptionally abundant, or, from a more enlightened ecosystem approach, such "wastage" may be viewed as carrion enrichment for a diverse community of scavengers.

Program Options

The "WOLF" program offers seven options for the user. Four of these are management alternatives, and three of these address future weather conditions and anticipated wolf behavior. For each option, a screen is presented which describes the available alternatives. Below, the alternatives are listed for each option and the computational consequences resulting from the choice of each alternative are explained. Because the combination of alternatives are numerous, a justification for the "default" selection for each choice for the purpose of comparing simulation results is presented. The default alternatives for each option are summarized in Table 2.

Table 2. Default responses to options in the "WOLF" program.

Option	Default Alternative
Winter Severity	Average Winters
Migratory Behavior	Partial Migrations
Elk Hunt	Continue Elk Hunt
Conflicts w/Humans	Wolves Avoid Humans
Legal Wolf Culls	Wolves Culled Outside Park
Poaching in Park	Little Poaching Mortality
Inoculum Size	30

Option #1: Weather Conditions

The screen reads:

> The period 1981-88 had mild winters which allowed ungulate populations to achieve high densities in the park. This option allows you to select weather conditions equal to the average observed during this century, or you may select 10% more severe, or 10% milder than average winters for the next 100 years. This last alternative may be particularly relevant if the greenhouse effect continues to warm the planet.
>
> Choose one of the following and type the number of your choice:
> 1 = AVERAGE CLIMATIC CONDITIONS; 2 = SEVERE WINTERS; 3 = MILD WINTERS.

Choosing severe or mild winters results in a winter severity index that is increased or decreased respectively by 10%. The standard deviation in winter severity remains exactly the same, only the mean is changed. Increased winter severity reduces ungulate numbers over the long run, which ultimately reduces average wolf numbers as well. The opposite is true for mild winter conditions.

Although one might make a strong case for global warming, the most plausible selection for this choice is that average climatic conditions will prevail.

Option #2: Migratory Behavior of Wolves

The screen reads:

> In some regions wolves are known to migrate in pursuit of prey, e.g., after some caribou (Rangifer caribou) herds. We cannot predict if wolves will migrate following elk and bison or if they will remain resident on winter ranges year-round. The most likely scenario seems to be moderate levels of migration, becoming more pronounced over the years as the wolves become acclimated to the Yellowstone ecosystem.
>
> Choose one of the following and type the number of your choice:
> 1 = NONMIGRATORY; 2 = PARTIAL MIGRATIONS.

Migratory behavior increases potential carrying capacity for wolves on their winter range. For nonmigratory wolves, the carrying capacity (K_{wolf}) is set at 150 wolves, whereas it is set at 200 wolves for partially-migratory wolves. The nonmigratory wolf carrying capacity was estimated from Figure 2 while assuming that at least one-half of the territories would occupy ungulate winter

range as outlined by Houston (1979). The consequence of selecting the migratory behavior alternative is an increase by six packs in the carrying capacity for wolves in the park.

Partial migrations are likely to develop quite rapidly as wolves seek prey which migrate seasonally (Shoesmith 1979). Apparently such seasonal movements by wolves occurred historically (Weaver 1978). My "default" choice here is partial migrations.

Option #3: Elk Hunt

This time the screen reads:

> Currently, the Montana Department of Fish, Wildlife and Parks manages winter elk and bison hunts in Paradise Valley immediately north of the park. Particularly in severe winters, hunter kill of elk may be sizable. In future years, permits for the late hunts will be limited to 700. For this simulation, you are afforded the responsibility of deciding to continue the elk hunting season or closing it.
>
> Choose one of the following and type the number of your choice:
> 1 = CLOSE THE HUNT; 2 = CONTINUE THE ANNUAL ELK HUNT.

In the "WOLF" program, additional elk are added to the population each year if it is determined that the elk hunt should be terminated. Background data are based upon an elk population that has been hunted, and hunting mortality contributes to density-dependent mortality in the herd. It seems likely that the Montana Department of Fish, Wildlife and Parks will discontinue hunting if elk numbers reach exceptionally low levels. Therefore, a lower threshold of 5,000 elk has been set below which the hunt will be stopped automatically even if alternative 2 is selected.

Future permit quotas are set at 700 elk. Assuming 78% mean hunter success and 10% crippling loss, the total number of elk killed by hunters during the late hunting season will average approximately 600 animals.

It would be impolitic to close the hunt in Paradise Valley; therefore, the most plausible selection is alternative 2, to continue the hunt.

Option #4: Will Wolves Avoid Humans?

For this choice, the screen reads:

> Experiences in northern Minnesota suggest that wolves will usually avoid contact with humans. However, occasionally wolves lose fear of man and are more likely to come into conflict with ranchers, campers, and others who might intentionally or unintentionally harm wolves. We cannot predict how the introduced wolves will behave. What is your guess?
>
> Choose one of the following and type the number of your choice:
> 1 = WOLVES WILL AVOID HUMANS AND SETTLEMENTS; 2 = CONFLICTS WITH MAN WILL BE FREQUENT.

In alternative 2, the wolf mortality rate has been arbitrarily increased by 15%. This mortality rate is expected to include both illegal poaching mortality as well as a higher level of damage control removals.

There will certainly be occasional conflicts with man, and dispersing wolves will sometimes kill livestock (Fritts et al. 1984). Indeed, when the wolf population becomes saturated, a 15%-25% dispersal of wolves out of the park each year may be anticipated (L. D. Mech pers. comm.). Yet, because native prey are so abundant in the Yellowstone ecosystem, the default is alternative 1.

Option #5: Will Legal Wolf Kills Be Allowed?

The screen reads:

> A possible management option is that wolves leaving Yellowstone National Park will be killed to minimize potential conflicts with ranching and game management. It is also possible that legal sport hunting and/or trapping for wolves could be allowed. You may select total protection for wolves except for repeated offenders, or you may select open season on wolves once they leave the boundaries of Yellowstone National Park.
>
> Choose one of the following and type the number of your choice:
> 1 = WOLVES WILL BE CULLED; 2 = WOLVES WILL ENJOY TOTAL PROTECTION.

As in option #4, if culling is selected, there will be a 15% increase in wolf mortality rate. The magnitude of this value is arbitrary.

Table 29. Mule deer harvest survey results for areas south of Yellowstone Park in District I, Wyoming, 1980-1988 (from Straley et al. 1982-1987; Moody et al. 1988; Lockman et al. 1989).

Year	Herd	Hunt Area	Number of Hunters	Harvest[a]				Percent Success
				Bucks	Does	Fawns	Total	
1980	Jackson	148	1176	107	74	-	181	15.4
		150	324	22	54	-	76	23.5
		155	520	36	11	-	47	9.0
		156	1272	107	146	-	253	19.9
	Targhee	149	344	70	15	-	85	24.7
1981	Jackson	148	996	69	82	-	151	15.2
		150	475	109	33	-	142	29.9
		155	690	59	65	-	124	18.0
		156	1745	254	64	-	318	18.2
	Targhee	149	461	57	50	-	107	23.2
1982	Jackson	148	1256	164	34	15	213	17.0
		150	160	3	0	0	3	1.9
		155	807	126	52	18	196	24.3
		156	2056	288	137	26	451	21.9
	Targhee	149	744	96	29	0	125	16.8
1983	Jackson	148	745	85	45	-	130	17.4
		150	112	11	0	-	11	9.8
		155	650	58	19	-	77	11.8
		156	1519	134	126	-	260	17.1
	Targhee	149	575	76	29	-	105	18.3
1984	Jackson	148	727	117	21	-	138	19.0
		150	102	15	0	-	15	14.7
		155	581	104	21	-	125	21.5
		156	1193	111	30	-	141	11.8
	Targhee	149	283	42	14	-	56	19.8
1985	Jackson	150	72	12	0	0	12	16.7
	Targhee	149	194	25	0	0	25	12.9
1986	Jackson	150	25	7	0	0	7	28.0
	Targhee	149	204	33	0	0	33	16.2
1987	Jackson	150	33	7	0	0	7	21.2
	Targhee	149	210	61	0	0	61	29.0
1988	Jackson	150	33	5	0	0	5	15.2
	Targhee	149	187	63	0	0	63	33.7

[a] Unless indicated by actual numbers, does and fawns were grouped together as does.

The inoculum size can be critical simply because, with a small number of wolves released, there is a good chance that none will settle in the park. Dr. L. David Mech (pers. comm.) found that an initial release of 30 wolves would offer a reasonable chance that wolf recovery would be effective, and releases of young wolves may be best. However, it may be difficult to obtain 30 wolves in one year, and thus, for logistical reasons, releases may need to be spread over a longer period of time. Furthermore, it may be necessary to supplement the wolf population in early stages of wolf recovery if it appears that an early inoculum is not taking.

Spatial Distribution of Wolf Packs

The final screen of the model output is a map of Yellowstone National Park showing the anticipated locations of wolf packs in the park, depending upon the average number of wolves projected through the next century. The appropriate map is accessed by the core Turbo Pascal program. Each of the 20 maps was generated by digitizing a photocopy of a map of Yellowstone National Park using a Houston Instruments High Pad digitizer. Maps were enhanced using FREELANCE and stored individually to be accessed, depending upon the number of wolf packs calculated to exist in the park.

RESULTS

Ungulate Population Dynamics Without Wolves

Perhaps the most striking outcome of ungulate population projections under the "WOLF" program is the high variance in population size through time. Yet, this result is empirically based. Variation in winter severity causes substantial population fluctuations in all ungulates in the greater Yellowstone ecosystem, and such fluctuations are well documented (Meagher 1971, Houston 1982). For example, in 1989 a decrease in elk numbers by an estimated 8,000-10,000 due to density dependence, hunting, drought, fire, and slightly above average winter severity was observed (Singer et al. 1989, Singer and Schullery 1989, Boyce and Merrill 1990).

Average population sizes for elk and wolves tend to be lower in the stochastic model simulations than for deterministic calculations using the same parameter values (Table 3). Lower average population size is due to reduced long-term population trajectories in stochastic simulations (Boyce 1977) as well as to the general concavity of population growth rate in these density-dependent models (Boyce and Daley 1980).

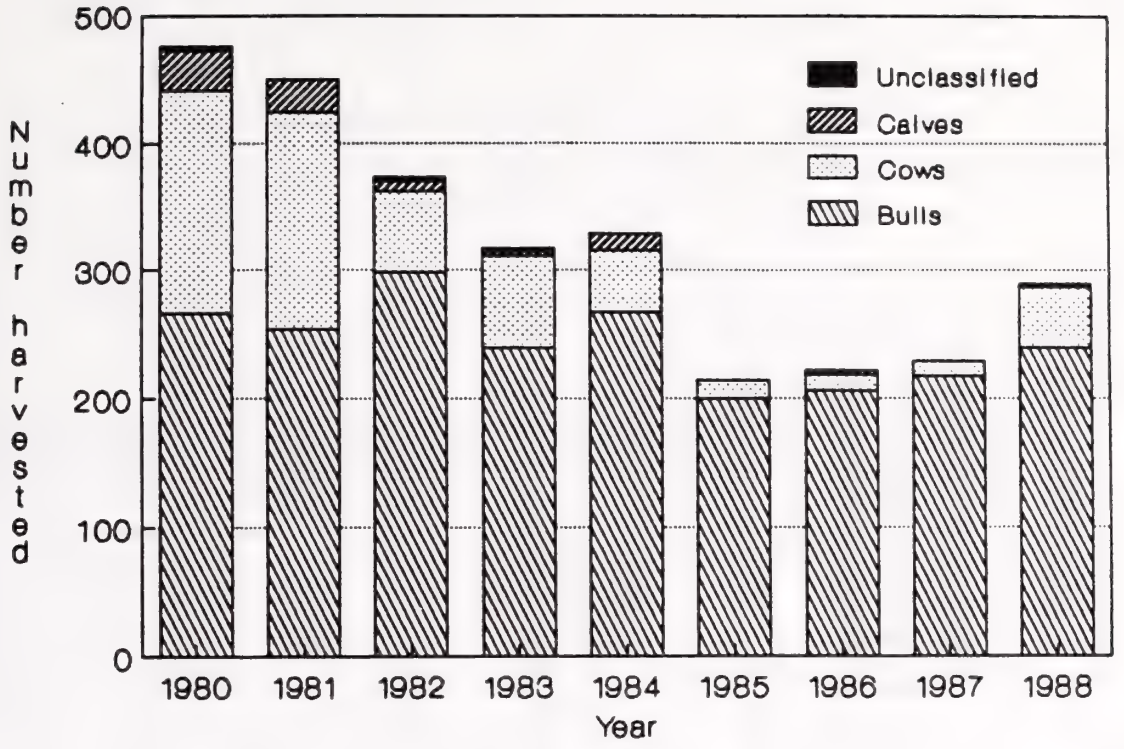

Fig. 53. Classification of the moose harvest (bulls, cows, calves, and unclassified) for the Jackson herd unit in Wyoming south of Yellowstone Park, 1980-1988 (adapted from Straley et al. 1985, Lockman et al. 1989).

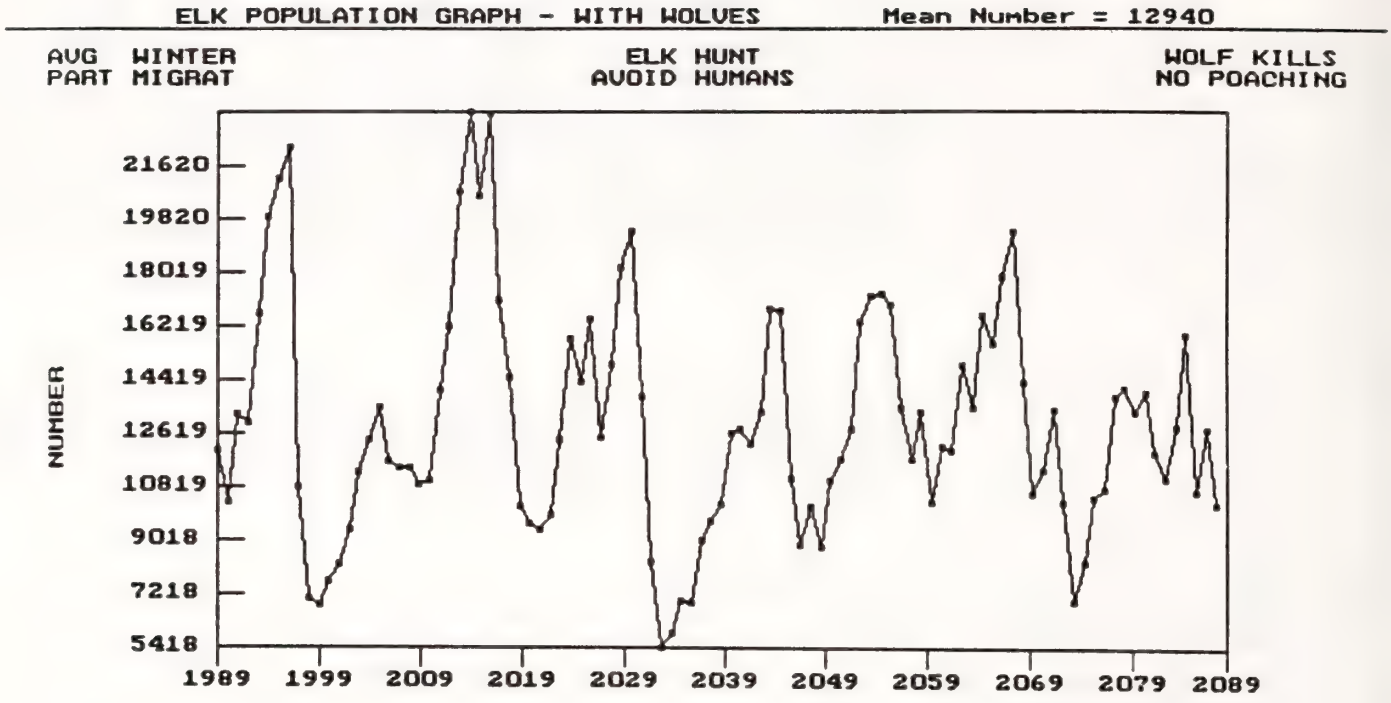

Fig. 4. Typical population projection for elk using default alternatives defined in Table 2.

Table 30. Moose harvest survey results for areas south of Yellowstone Park in District I, Wyoming, 1980-1988 (from Straley et al. 1982-1987; Moody et al. 1988; Lockman et al. 1989).

Year	Herd	Hunt Areas	Number of Permits	Number of Hunters	Harvest					Percent Success
					Bulls	Cows	Calves	Unclass.	Total	
1980	Jackson	7,14,15,	596	587	266	175	31	4	476	81.0
1981[a]		17-19,28,	568	559	254	171	31	0	450	80.5
1982		28,32,20N	575	553	298	64	8	3	373	67.0
1983			490	479	240	71	3	3	317	66.1
1984			485	478	267	48	13	0	328	68.6
1985			300	287	200	14	0	0	214	74.5
1986			325	312	206	13	3	0	222	71.2
1987			290	287	218	11	0	0	229	79.8
1988			350	342	240	47	2	0	289	84.5
1980	Targhee	16,37	35	35	27	2	0	0	29	83.0
1981			35	33	21	1	0	0	22	66.7
1982			35	34	25	3	3	0	31	91.1
1983			35	35	23	3	2	1	29	82.9
1984			40	40	32	0	0	0	32	80.0
1985			40	40	32	6	0	0	40	100.0
1986			40	40	27	6	1	0	34	85.0
1987			45	45	37	5	1	0	43	95.6
1988			65	62	29	17	4	0	50	80.6

[a] Hunt area 20N was closed after 1981.

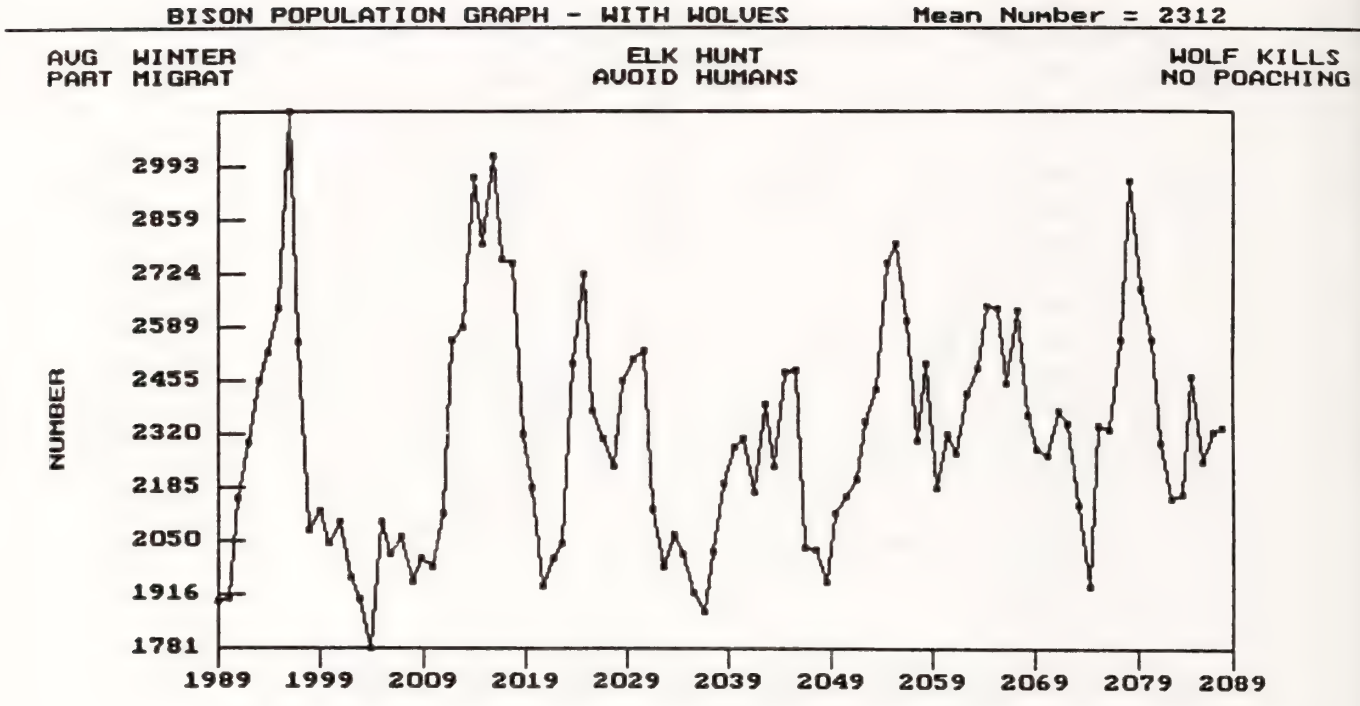

Fig. 5. Typical population projection for bison using default alternatives defined in Table 2.

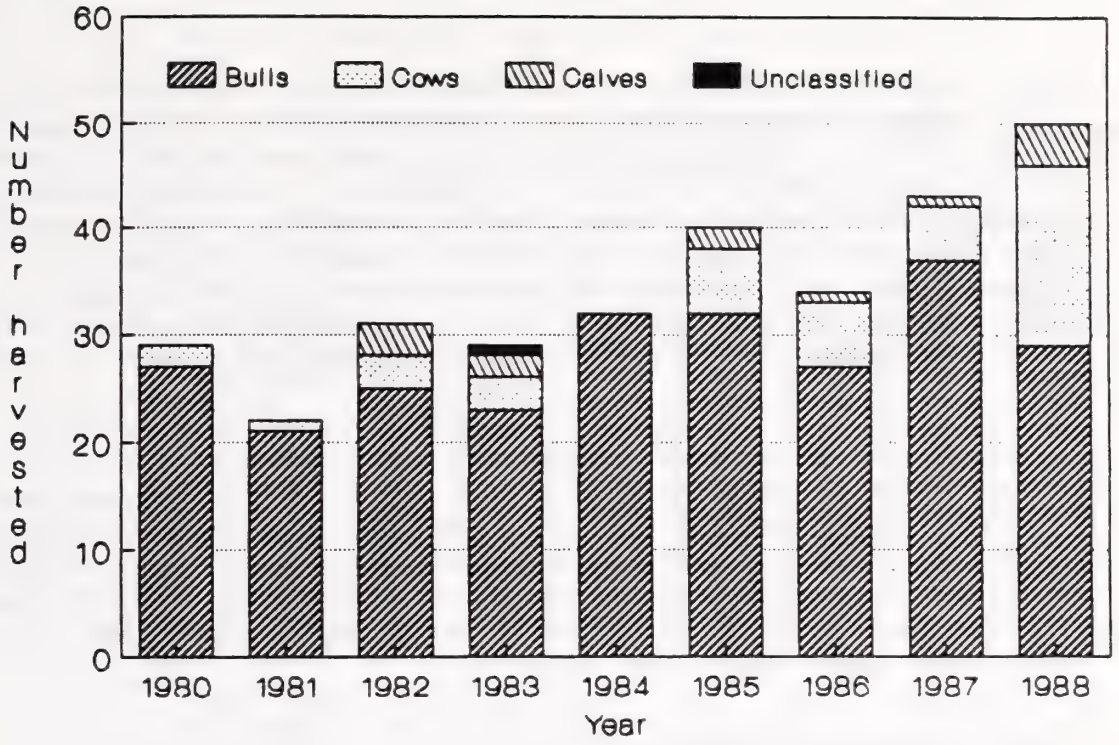

Fig. 55. Classification of the moose harvest (bulls, cows, calves, and unclassified) for the Targhee herd unit in Wyoming south of Yellowstone Park, 1980-1988 (adapted from Straley et al. 1985, Lockman et al. 1989).

Although wolves preferred mule deer slightly more than elk, the number of deer killed by wolves is fewer than elk because they have a lower population size. The effect of wolf predation on both mean population size and variance in population size of mule deer is intermediate between that of elk and bison. Simulations suggest a reduction by 10%-15% in mule deer numbers and a reduction in the relative variability in deer numbers, reflected by a decline in the coefficient of variation in mean numbers by 20%-25%. The number of mule deer from a typical run from the "WOLF" program is presented in Figure 7. Response of deer numbers to management alternatives are presented in Table 3.

When building the model, there was the concern that there may be a risk that deer could be extirpated by wolves. Yet, a risk was unlikely because there should always be some deer near the town of Gardiner, Montana, where a number of deer winter. This risk motivated the construction of a refuge in the "WOLF" program to ensure that wolves did not reduce deer numbers below 700. As it turned out, however, wolf predation on deer is not likely to drive deer numbers anywhere near the refuge level.

Wolf Population Dynamics

Under most management scenarios, between 50 and 120 wolves are expected to be found in Yellowstone National Park during the century following reintroduction. Three of the options offered the users of the "WOLF" program involve an increase in the mortality rate for wolves, i.e., frequent conflicts with man, culling outside of the park, and poaching within the park. Future wolf populations are highly sensitive to these options (Table 3). If the user chooses to increase mortality in all three options, the survival rate for wolves would be:

$$(1 - 0.15)(1 - 0.15)(1 - 0.2) = 0.578 \qquad \text{(equation 10)}$$

of that occurring without the human-induced mortality and the wolf population will decline and usually become extinct within a few years. This result is consistent with the observations of Keith (1983) and Ballard et al. (1987) that wolf kills by man in excess of 40% caused a decline in wolf populations.

Users of the "WOLF" program will note that it is common to observe low frequency oscillations in the number of wolves (Figs. 8 and 9). These oscillations are suggestive of nonlinear dynamics typical of some predator-prey systems. In deterministic simulations, no such oscillations appear and the system converges on equilibrium. Apparently the stochastic variation is great enough to destabilize the system temporarily. The population then undergoes transient motion back toward a stochastically varying equilibrium. No way to study the dynamical behavior of such transient motion to determine how it might be attributed to system nonlinearities is known.

Table 31. Bighorn sheep harvest survey results for areas south of Yellowstone Park in District I, Wyoming, 1980-1988 (from Straley et al. 1982-1987; Moody et al. 1988; Lockman et al. 1989).

Herd	Hunt Area	Year	Number of Permits	Number of Hunters	Total Rams	Percent Success
Jackson	7	1980	24	23	7	30.4
		1981	24	24	13	54.1
		1982	24	21	14	66.7
		1983	24	22	10	45.4
		1984	28	28	17	60.7
		1985	28	27	21	77.8
		1986	33	33	13	39.4
		1987	33	33	14	45.2
		1988	32	32	16	50.0
Targhee	6	1980	8	4	2	50.0
		1981	8	8	1	12.5
		1982	8	7	2	28.6
		1983	8	-	0	0.0
		1984	8	7	1	14.2
		1985	4	4	1	25.0
		1986	4	4	2	50.0
		1987	4	3	0	0.0
		1988	4	2	0	0.0

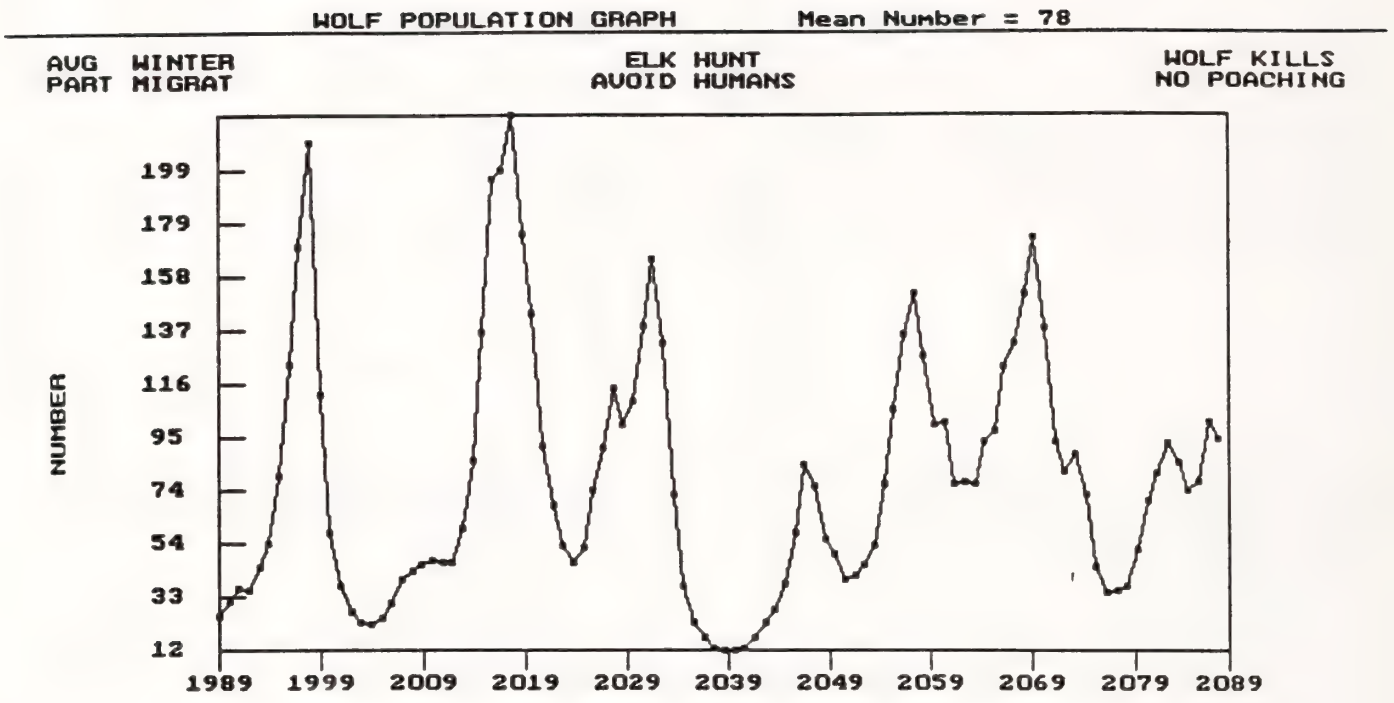

Fig. 8. Typical population projection for wolves using default alternatives in Table 2.

Classification data was collected for the Targhee herd from 1980 to 1986. Population numbers were stable to increasing but should be considered rough estimates (Table 36). Fawn/100 does ratios appear to be relatively high for this herd unit judging from classification data collected in 1987 and 1988 (Table 37).

Moose

Moose population estimates for the Jackson herd unit declined from 1980 to 1984 and increased from 1985 to 1988. However, trend counts of moose have generally increased (Table 38). Some of the trend count increases were attributed to using a helicopter (instead of fixed winged aircraft as was the case in 1980) and increased flight time. The dramatic increase in the 1983 trend count compared to 1982 was attributed to deeper snows and increased helicopter flight time.

High hunter success, even with increasing harvests, suggests the population is increasing in the Targhee moose herd unit. (Moody et al. 1988, Table 40). No aerial trend counts were conducted for this herd unit. Classification data were collected from hunter surveys between 1980 and 1985 (Table 41). Calves/100 cows ratios were variable but appeared to be increasing through 1985. The bull ratios were variable with no apparent trend. Aircraft classification data collected from a helicopter in 1985, 1987, and 1988 (Table 41). Bull and calf ratios were variable and more data are needed to establish a trend.

Bighorn Sheep

Preseason classification data were obtained from hunter surveys for the Jackson bighorn sheep herds between 1981 and 1984 (Table 42). After 1984, no preseason data were collected.

Table 33. Elk classification data collected in 1987 and 1988 for the Targhee herd unit in Wyoming, south of Yellowstone National Park (Lockman et al. 1989).

Year	Bulls/ 100 Cows	Spikes/ 100 Cows	Calves/ 100 Cows	Number Classified
1987	20	14	52	82
1988	41	11	57	147

Spatial Distribution of Wolf Packs

The maps showing the distribution of wolf packs throughout Yellowstone were created based upon the current winter distribution of ungulates within the park and the historical distribution of wolf observations and den sites as reported by Weaver (1978). Since the majority of wintering ungulates occur on the northern range, it is expected that most wolf packs will occur there as well. An example of one of these maps corresponding to a wolf population with an average of 78 wolves in nine packs is presented in Figure 10.

Sensitivity Analysis

To understand the behavior of the "WOLF" program an appreciation for the sensitivity of various inputs is required. A sensitivity analysis focusing on variables of ecological significance including those variables for which reliable estimates were unavailable were performed. A summary of the analysis of the "WOLF" program is presented in Table 4.

In general, the population dynamics for wolves and elk govern the overall behavior of the model. Populations of ungulates and wolves are relatively unresponsive to perturbations of the functional and numerical responses for bison, moose, and deer, whereas all species exhibit response to perturbations in elk functional and numerical responses. In particular, a 20% reduction in F_{max} results in a 21% decline in the mean number of wolves. Similarly, a 20% reduction in the R_{elk}, the numerical response parameter, causes a 36% reduction in wolf numbers.

The parameters which created the greatest responses in ungulate population size were the carrying capacities for the respective species, K_is. The response to fires could exhibit great latitude without causing substantial change in either ungulate or wolf numbers.

The empirical basis for estimation of the functional response parameters, F_is, is probably the weakest. Fortunately, population projections were relatively insensitive to perturbation of the F_is, suggesting that substantial errors in estimation may not be of serious consequence to the outcome of population projections. In other words, the model is reasonably robust to variation in the placement of the functional response curves.

Sensitivity analysis based upon proportional perturbations of parameters tends to obscure the fact that some of the parameters may be relatively invariant in nature. For example, K_is for ungulates vary enormously in response to climatic influences on seasonal range conditions. In contrast, it is not known whether F_{max}s or F_is vary much at all. It is not only the proportional responsiveness to perturbation that matters in understanding the structure of the model, but also the ecological interactions that create variation in the parameters.

Table 34. Population trend counts and population estimates for mule deer as reported for the Jackson herd unit in Wyoming, south of Yellowstone National Park, 1981-1988[a] (adapted from Straley et al. 1985, 1986; Moody et al. 1988; Lockman et al. 1989).

Year	Trend count	Population estimate
1981	140	200
1982	165	230
1983	235	270
1984	180	275
1985	250	300
1986	276	325
1987	---	340
1988[b]	---	700

[a] From 1981 to 1984, the Jackson herd unit trend counts included hunting areas 148, 150, 155, and 156. The boundaries for this herd unit were changed in 1985 and only mule deer herd statistics from hunting area 150 were considered and recalculated back to 1981.

[b] Hand calculations using the classification data were used to estimate the population in 1988.

Table 35. Mule deer classification for the Jackson herd unit in Wyoming, south of Yellowstone National Park, 1981-1988[a] (adapted from Straley et al. 1985, Lockman et al. 1989).

Year	Bucks/ 100 does	Fawns/ 100 does	Total Classified
1981	28	54	121
1982	44	80	122
1983	30	68	220
1984	39	89	151
1985	32	86	211
1986	45	98	236
1987	45	84	280
1988	47	99	211

[a] From 1981 to 1984, the Jackson herd unit classification data included hunting areas 148, 150, 155, and 156. The boundaries for this herd unit were changed in 1985 and only mule deer herd statistics from hunting area 150 were considered and recalculated back to 1981.

Table 4. Sensitivity analysis of selected variables (Table 1.) in the "WOLF" program. The mean population size for comparison of perturbation responses is based upon deterministic projections. All perturbations entailed a decrease in the parameter value by 20%. Perturbation responses are expressed as a proportion of the state variables prior to perturbation.

Variable	N_{elk}	N_{bison}	N_{moose}	N_{deer}	N_{wolf}
Default (n = 30)	12634	2263	774	2878	76
Deterministic	13067	2244	779	2833	89
Perturbation Responses					
F_{max}(elk)	0.0811	0.024	0.009	0.03	-0.213
F_{max}(bison)	0	0.001	0	0	0
F_{max}(moose)	0	0	0	0	0.011
F_{max}(deer)	0	0	0	0	0.011
F_{elk}	0.053	0.014	0.006	0.018	-0.125
F_{bison}	0.006	0.023	0.001	0.003	-0.022
F_{moose}	0.001	0	0.009	0	0
F_{deer}	0.001	0	0	0.029	0
r_o(elk)	-0.031	0.008	0.003	0.01	-0.068
r_o(bison)	0.001	-0.02	0	0.001	0
r_o(moose)	0	0	-0.006	0	0
r_o(deer)	0.001	0	0	-0.026	0

Table 38. Population trend counts and estimates for the Jackson moose herd unit in District I, Wyoming south of Yellowstone National Park, 1980-1988 (adapted from Straley et al. 1985, Lockman et al. 1989).

Year	Trend count	Population estimate
1980	460	2200
1981	630	2000
1982	667	1800
1983	1043	1860
1984	877	1830
1985	1044	1950
1986	928	2030
1987	1146	2150
1988	1120	2300

Table 39. Hunter and aircraft classification data collected for the Jackson moose herd unit in District I, Wyoming south of Yellowstone National Park, 1980-1988 (adapted from Straley et al. 1985, Lockman et al. 1989).

Year	Hunter classification Survey			Aircraft classification Survey		
	Bulls/ 100 cows	Calves/ 100 cows	Total Classified	Bulls/ 100 cows	Calves/ 100 cows	Total Classified
1980	45	45	2967	60	49	460
1981	40	49	3184	38	47	630
1982	35	43	2705	37	42	667
1983	32	48	3104	46	53	993
1984	31	43	3677	52	52	877
1985	40	43	2145	44	46	1044
1986	--	--	----	43	49	928
1987	--	--	----	42	53	1146
1988	--	--	----	62	40	1065

DISCUSSION

Population regulation in the ungulates of Yellowstone National Park is viewed substantially the same as the nonlinear plant-herbivore model described by Caughley and Lawton (1981). The information available to develop a complete plant-herbivore model was inadequate; therefore, a trophic level is missing in the "WOLF" program. Because there are several species incorporated into the model, it is complex. Complex models, especially when driven by seasonal forcing (Inoue and Kamifukumoto 1984), can yield complex dynamics. However, our analysis of elk and bison population dynamics for the northern range herds showed no evidence of such complex dynamics, and indeed both species showed stable dynamics, contrary to the model presented by Eberhardt (1987). Population fluctuations were attributable to stochastic variation in winter severity and summer range phytomass but not due to inherent instability in the dynamics for either elk or bison.

The features of wolf population regulation in the "WOLF" program are similar to those characterized by Packard and Mech (1980, 1983). Specifically, population regulation in wolves results from an interaction of social and nutritional variables. Pack territoriality sets an upper limit to wolf population size which is only attained when prey abundance is exceptionally high.

Consequences of Management Alternatives

Potential Conflicts With Hunting

One of the major concerns about wolf recovery is the possibility that predation on ungulates will substantially reduce populations of hunted game species, especially elk, moose, deer, and bighorn sheep (Zumbo 1987). Simulation results indicate that there will be a reduction in the number of these game mammals, although it does not appear necessary that wolf predation require that hunting opportunities be reduced. Rather, the result will be to maintain lower populations of ungulates. In the same fashion that density dependence ensures sustained yield hunting opportunity, moderate predation by wolves results in compensatory mortality and natality.

Under the default alternatives, the "WOLF" program projects that terminating the late Gardiner hunt in Montana will only increase the wintering population of elk in Yellowstone by 7%. Interestingly, the increase in the elk population is accompanied by a 20% reduction in the coefficient of variation in mean elk numbers. This reduction occurs because of the way that the elk hunt was modeled. For the "WOLF" program, it was presumed that the Montana Department of Fish, Wildlife and Parks will continue to annually issue 700 elk permits for the late Gardiner hunt. The number of permits issued would only change if the population of elk fell below 5,000 animals, whereupon the elk hunt would be temporarily discontinued. In reality, it seems probable that if elk numbers again become exceptionally high, as they were in 1988, the number of permits

Postseason classification data showed lamb/100 ewes ratios steadily declined from 1980 to 1984 and averaged 46 lambs. The lamb ratio increased dramatically in 1985, dropped in 1986 and remained relatively constant at 44 lambs/100 ewes between 1986 and 1988 (Table 42). Reasons for declining lamb ratios are not apparent but may be related to competition with other ungulates (Straley et al. 1983, Moody et al. 1988) and adverse weather conditions as in spring 1982 (Straley et al. 1983). Ram/100 ewes ratios steadily declined between 1980 and 1986 and appeared to stabilize between 1986 and 1988 (Table 42). This decline is related to a slightly increasing ram harvest and low lamb production (reducing the availability of new rams), particularly between 1982 and 1984. The population estimates for Jackson bighorns declined between 1980 and 1982 and slowly increased to approximately 550 sheep in 1988 (Fig. 58).

Between 38 and 58 sheep were counted during trend counts of the Targhee herd from 1980 to 1987 (Table 43). The most complete helicopter count in 1988 yielded 89 sheep. Comparisons with 1987 data are not possible because only a ground count was done in 1987 (Lockman et al. 1989). No population model was developed for this herd but population numbers estimated each year were 100 sheep from 1980 to 1987. From hand calculations of classification data, population numbers were estimated at 105 sheep in 1988 (Lockman et al. 1989).

Preseason hunter survey data were collected from 1980 to 1984 (Table 42) and show ram/100 ewes ratios declined from 88 in 1980 to 18 in 1984. The lamb/100 ewes ratios were quite variable. The low lamb ratio reported in 1982 may be influenced by adverse weather conditions contributing to increased lamb mortality (Straley et al. 1983).

Poaching

Poaching was incorporated as an option in the "WOLF" program because local ranchers have said that they will poison wolves inside the park, if wolves are reintroduced into Yellowstone. Poaching could be a serious problem and significantly reduce the chance of an effective wolf recovery. Poaching would be much more of a threat to the continued survival of wolves in the park than legal culling of wolves outside the park, because legal culling would not threaten wolves in packs whose complete home range was within Yellowstone.

Initial Inoculum

Inoculum size has a major bearing on the likelihood for success of wolf recovery. Vagaries of the environment and of wolves' behavior require that a fair number of wolves be released if a reasonable number are to establish territories. U.S. Senator James McClure (ID) has proposed releasing three pairs of wolves (Thuermer 1989), which my model suggests may have only a modest chance of surviving. There are tradeoffs, however. The more wolves that are released initially, the greater the number of conflicts that are likely to arise with livestock growers in the area. Wolves are likely to disperse subsequent to initial release (Fritts et al. 1984). Perhaps a higher risk of extinction is an acceptable price to pay for greater public acceptance of the wolf recovery program. Also, the McClure proposal allows for additional releases of wolves if the original three pair do not survive.

Recovery Zone for Wolves

These simulations only attempt to include ungulates and wolves within the confines of Yellowstone National Park. The probability of a successful wolf recovery could arguably depend a large part on the management that takes place in areas surrounding the park. For example, if wilderness areas and national forests surrounding the park are included in the recovery zone, the total number of wolves in the Yellowstone ecosystem could be much higher. Along with this increase in carrying capacity for the wolves comes a lower probability of extinction.

Based upon the sketchy data available, an exact estimate for the probability of extinction of wolves in the greater Yellowstone ecosystem is unable to be offered. However, simple models exist which estimate the extent to which expanding the recovery zone will enhance the probability of persistence of wolves in the greater Yellowstone ecosystem.

A variety of approaches have been used to model extinction. Small populations disappear, on the average, more quickly than larger ones for whom the impact of chance events may be all but negligible. Simulations using the "WOLF" program fairly frequently end with the wolf population becoming extinct. Clearly, the projected wolf populations have not achieved a secure level.

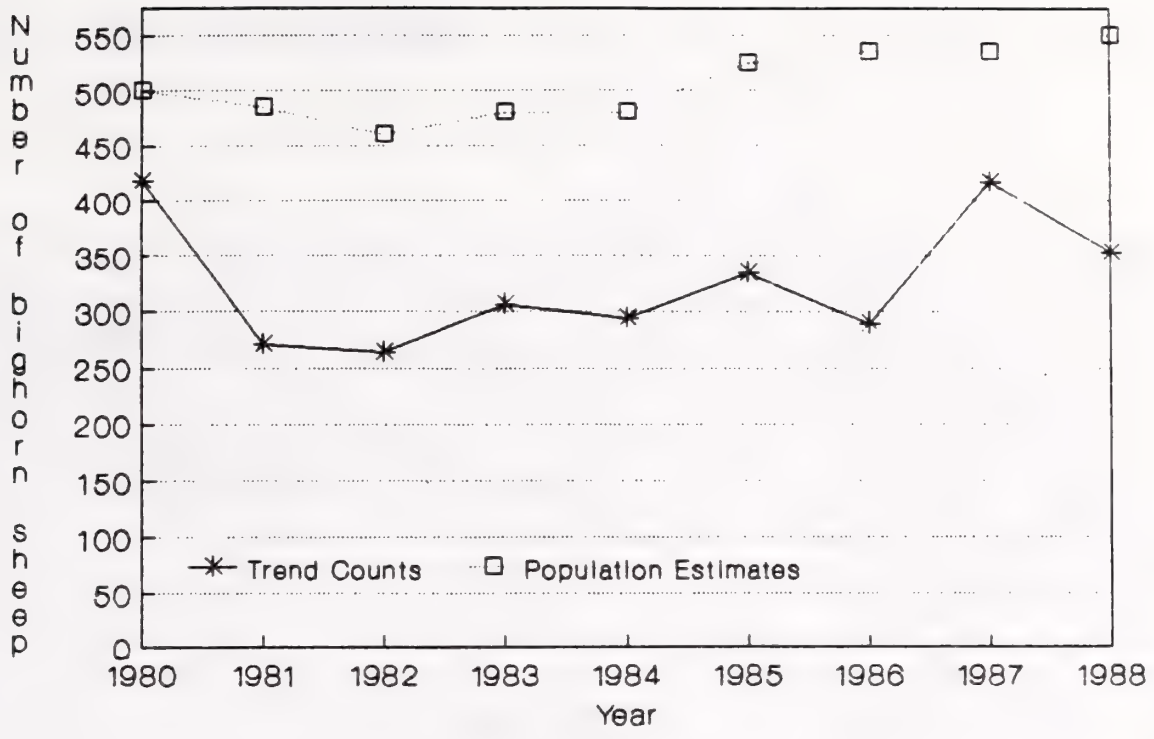

Fig. 58. Bighorn sheep population estimates and trend counts for the Jackson herd unit in Wyoming south of Yellowstone Park, 1980-1988 (adapted from Straley et al. 1985, 1986; Moody et al. 1988; Lockman et al. 1989).

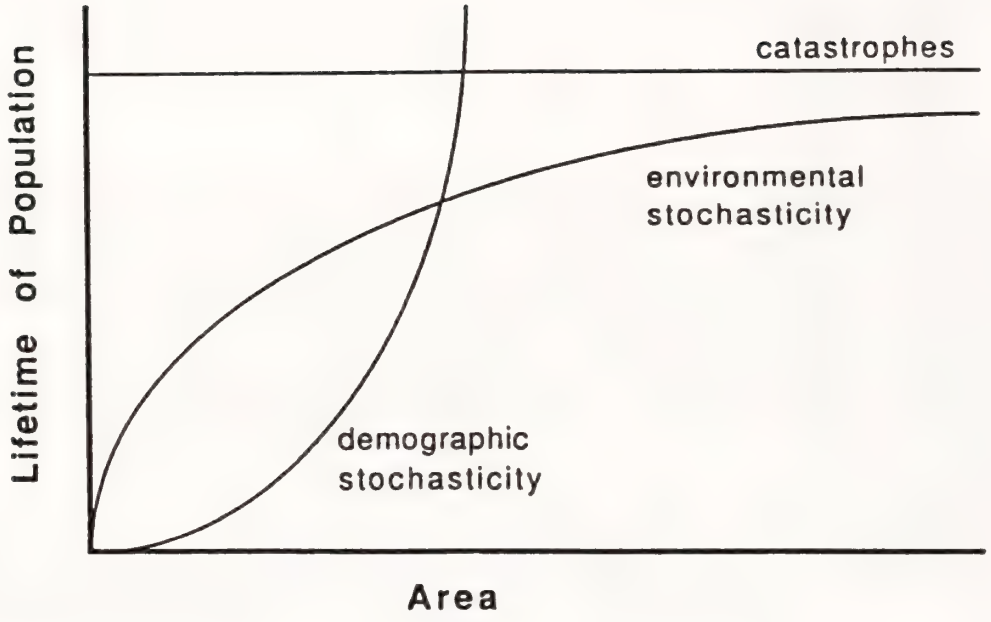

Fig. 11. Functional relationships between area of recovery zone and the lifetime of a population on it for three classes of stochasticity.

IDAHO SUMMARIES

Seasonal Ranges and Distribution

Elk

The Sand Creek elk herd occupies the area of Idaho adjacent to Yellowstone National Park. Brown (1985) and Vales (1989) estimated 76% of the Sand Creek herd occupied areas east of Highway 20 (including Yellowstone N.P.) during the summer. Twenty-four percent of the Sand Creek herd migrated into Yellowstone National Park each summer (Brown 1985, Fig. 59). Spring migrations to summer ranges lasted about 46 days (Brown 1985). Most calving occurred enroute to Yellowstone Park summer ranges, except when spring snows were shallow. Therefore, few newborn elk calves would be available for wolves during typical springs in Yellowstone. Brown (1985) estimated Yellowstone elk remained on summer ranges an average of 138 days (150 days, J. Naderman, Idaho Fish and Game Dept., pers. comm.) while those in Harriman State Park stayed on summer ranges 168 days. Fall migrations to the Sand Creek winter range lasted about 27 days (Brown 1985). The Sand Creek elk herd migrates through sagebrush flats to the Sand Creek winter range located west of the town of Rexburg and north of Idaho Falls. Additional elk from Yellowstone National Park and areas southwest of the park, winter on Conant Creek, Upper Teton River Canyon, Bitch Creek, Badger Creek, and the Falls River (J. Naderman, pers. comm.).

Mule Deer

Mule deer from the northeastern area of Idaho adjacent to Yellowstone National Park primarily winter in the Junipers-Sand Creek winter range. The deer from the Junipers-Sand Creek area migrate into the Island Park area, adjacent areas of the Targhee herd unit in Wyoming, and a few into Yellowstone Park during the summer.

Moose

Moose from five different wintering units in Idaho migrate in a northeasterly direction in the spring (Ritchie 1978, Fig. 60) to summer in areas east of Highway 20, southwestern Yellowstone National Park, and southwestern Montana. In particular, the Falls River moose herd summers and winters primarily east of Highway 20. Studies of tagged moose suggested equivalent numbers of Falls River moose summered in Idaho and Wyoming (Ritchie 1978). A few moose winter in Bechler Meadows in Yellowstone Park.

Hunting Season Regulations

Five hunt units (60, 60A, 61, 62, and 62A) from Region 6 in Idaho (headquarters in Idaho Falls) are located adjacent to the southwestern corner of Yellowstone

Computer simulations indicate that wolf recovery will result in a reduction in both the mean and variance in ungulate numbers. This reduction does not imply that management problems associated with elk and bison populations in the park will disappear. For example, the number of bison on the northern range will certainly not be reduced so low that seasonal movements north of the park (Meagher 1989a, 1989b) will be curtailed. Also, substantial die-offs of ungulates will continue to be observed during severe winters, although the magnitude of these should be less with wolves present.

The perception that the northern range is "overgrazed" may change subsequent to wolf recovery. Ungulates will continue to concentrate on the same ranges, since these are areas of lower snow accumulation where forage is more readily available. Yet, it seems likely that these areas have been heavily grazed by ungulates since the Pleistocene, and recent palynological (pollen analysis) evidence suggests that there have been no trends in vegetation composition on the northern range during the last 11,000 years (Barnosky et al. 1990).

Livestock conflicts resulting from wolf recovery have not been modeled. However, after wolves have become established, approximately 15-25 wolves may be expected to disperse from Yellowstone National Park each year. Some of these dispersing wolves will probably get themselves into trouble. Conflicts are likely to be most severe following initial release because translocated wolves are likely to disperse (Fritts et al. 1984). It is probable that some wolves will kill livestock and control of problem animals will be necessary.

Wolves will compete for game with hunters, and there will be differences of opinion as to whether wolves or hunters should be given priority. Hunters have mixed opinions on whether wolf recovery is good or bad. The Wyoming Guides and Outfitters Association has no official policy on wolf recovery because there is so much dissention among their members. Some members reflect Zumbo's (1987) view that hunting opportunities may decline as a consequence of competition between hunters and wolves. However, other members see benefits from wolf recovery. One guide believed that his business depended upon providing clients with high-quality wilderness experiences in the Teton Wilderness. What could be a higher quality wilderness experience than to hear wolves howling on the evening before embarking on a remote-country elk hunt?

Again, this model purpose is neither to encourage nor to discourage wolf recovery. The model is to be used to assist resource managers in making policy related to wolf recovery.

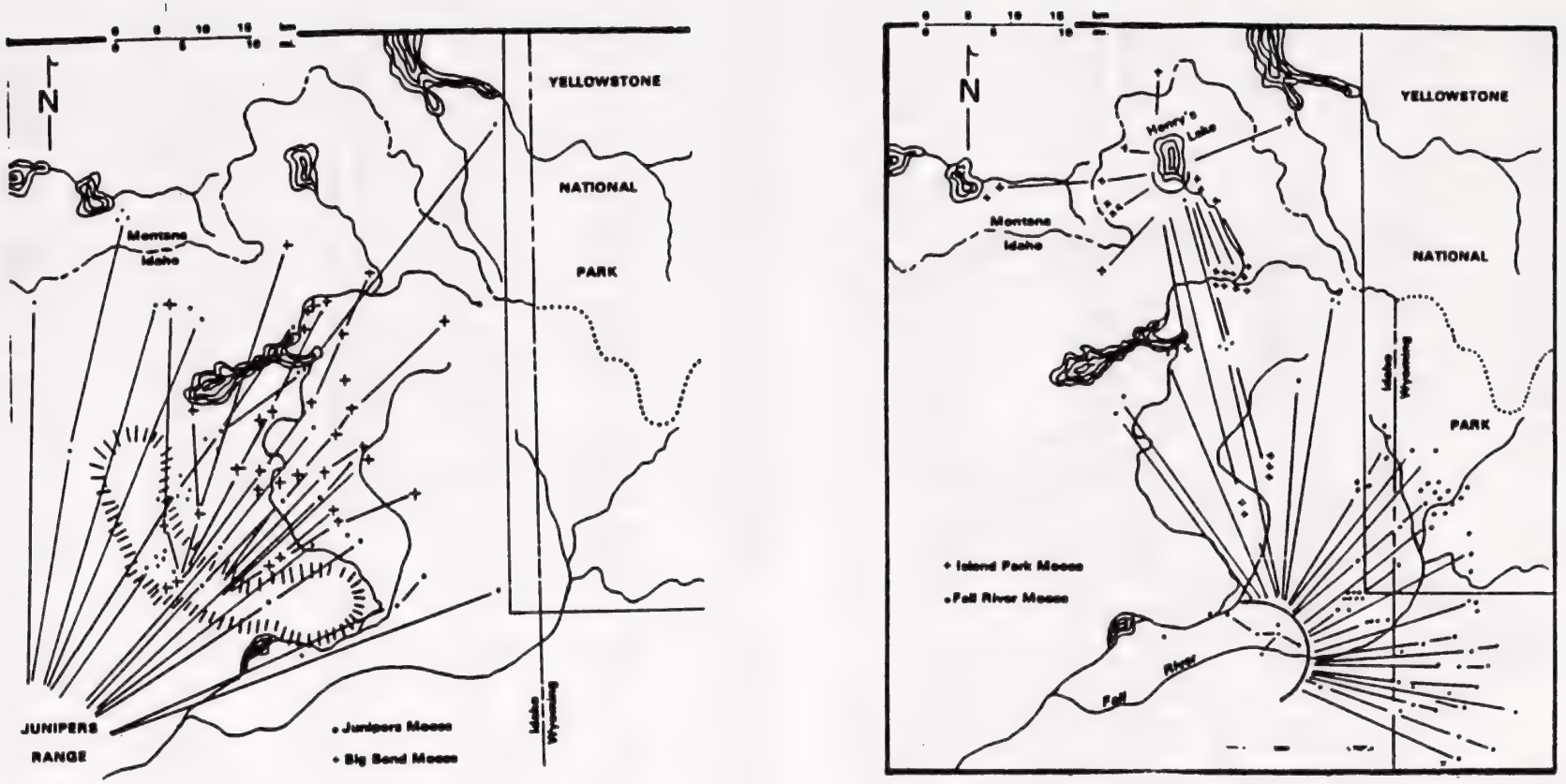

Fig. 60. Location of summer sightings for moose tagged on 4 Idaho winter ranges (Junipers, Big Bend, Fall River, and Henry's Lake) adjacent to southwestern Yellowstone Park. Figures are from Ritchie (1978).

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Fig. 61. Boundaries of 5 hunt units (60, 60A, 61, 62, 62A) in Region 6, in Idaho adjacent or near southwestern Yellowstone Park.

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Only hunt unit 61 offered a muzzleloader season from 1980 to 1988. In 1980 and 1981, either-sex deer could be harvested and the season lasted from 25 October to mid November. In 1982 and 1983, split seasons were held in which either-sex deer could be harvested for two days at the end of October. Only antlered bucks could be harvested for the first two weeks in November. In 1984 and 1985, antlered bucks could be harvested from the last week in October to the second week in November. In 1985 the season was expanded and either-sex deer could be harvested on 26 and 27 October. From 1986 to 1988, either-sex deer could be harvested from the last week in October to the third week in November.

Split general rifle seasons were held for most hunt units for all years between 1980 and 1988 except 1984. In 1980 and 1981, a 5 day either-sex season began the third week in October and a 5 day antlered buck season began the fourth week in October. In 1982, the antlered buck season was allowed during the third week in October and the either-sex season was allowed during the fourth week. Between 1983 and 1988, antlered bucks could be harvested from the second week to third week in October and then again for the first 2 weeks in November. An either-sex season, about 5 days long, began the fourth week in October.

Moose

From 1980 to 1988 a controlled hunt regulated the moose season. A special permit, obtained through a drawing was required to legally harvest a moose. From 1980 to 1988, only antlered moose could be harvested. Seasons were long, lasting from the first week in September until the first week in November.

From 1980 to 1982, moose hunting was allowed only in hunt unit 61. The total permits increased from 4 in 1980 to 8 in 1981 and 1982. From 1983 to 1985, moose hunting was expanded and included hunt units 60, 61, 62, and 62A. Total permits increased from 42 in 1983 to 57 in 1985. Moose hunting was again expanded beginning in 1986 when hunt unit 60A was added. Total permits remained stable at 68 from 1986 to 1988.

Harvest Summaries

Elk

Idaho's Sand Creek elk herd is harvested at high levels (Table 44). Hunter densities are as high as 5.1 hunters per km^2 during the general season. High densities of roads and timber cutting make elk highly vulnerable to hunting (Parker et al. 1986). A significant correlation was found between road density and percent yearling bulls in the harvest (Parker et al. 1986). Concern has been expressed that the harvest rates on bull elk may be approaching levels detrimental to herd productivity (Parker et al. 1986). Harvest levels are associated with severe weather. When adverse weather conditions force elk to migrate to winter ranges prior to the hunting season, more elk are harvested (Parker et al. 1986).

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Table 45. Deer harvest survey results for areas southwest of Yellowstone Park in Region 6, Idaho, 1980-1988 (from Kuck et al. 1989).

Year	Hunt Unit	Number of Hunters	Total Harvest	Percent			Numbers of			
				Success	Bucks	Does	Bucks	Does	Mule Deer	White-tailed Deer
1980	60	2840	532	19	-	-	-	-	-	-
	61	1910	379	20	-	-	-	-	-	-
	62	948	188	20	70	30	132	56	-	-
	62A	299	140	47	-	-	-	-	-	-
1981	60	1542	80	5	-	-	-	-	-	-
	61	2537	548	22	-	-	-	-	-	-
	62	690	183	26	56	44	102	81	-	-
	62A	548	203	37	-	-	-	-	-	-
1982	60	2114	868	41	94	6	816	52	-	-
	61	950	147	16	78	22	115	32	-	-
	62	721	262	36	75	25	197	65	-	-
	62A	262	16	6	0	100	0	16	-	-
1983	60	1552	386	25	48	52	186	200	343	43
	61	1224	154	13	71	29	110	44	143	11
	62	852	151	18	78	22	117	34	134	17
	62A	271	71	26	67	33	47	24	71	0
1984	60	919	159	17	100	0	159	0	159	0
	60A	131	38	29	100	0	38	0	38	0
	61	656	0	0	0	0	0	0	0	0
	62	430	24	6	100	0	24	0	24	0
	62A	278	17	6	100	0	17	0	17	0
1985	60	1161	498	43	34	66	169	329	483	15
	60A	422	203	48	62	38	126	77	203	0
	61	1438	309	21	63	37	195	114	309	0
	62	513	145	28	37	63	54	91	154	0
	62A	182	52	28	100	0	52	0	52	0
1986	60	1432	342	24	62	38	212	130	342	0
	60A	435	55	13	100	0	55	0	55	0
	61	981	125	14	57	43	71	54	125	0
	62	623	142	23	78	22	111	31	126	16
	62A	161	64	40	100	0	64	0	64	0
1987	60,61 62A	2488	632	26	80	20	506	126	-	-
1988	60	1380	696	50	53	47	369	327	640	56
	60A	546	310	57	75	25	232	78	298	12
	61	1226	497	41	66	34	328	169	457	40
	62	844	460	55	67	33	308	152	446	14
	62A	247	112	45	89	11	100	12	87	25

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Table 46. Continued.

Year	Hunt Unit	Number of Permits	Number of Hunters	Bulls Harvested	Percent Success
1987	60	15	15	15	100
	60A	3	3	3	100
	61	12	12	12	100
		8	8	8	100
		2	2	2	100
		8	8	8	100
	62	5	5	5	100
		5	5	5	100
	62A	5	5	5	100
		5	5	5	100
1988	60	15	15	15	100
	60A	3	3	3	100
	61	12	12	12	100
		8	8	8	100
		2	2	2	100
		8	8	8	100
	62	5	5	5	100
		5	5	5	100
	62A	5	5	5	100
		5	5	5	100

[a] Hunt units 60, 61, 62, and 62A were closed 1980-1982.

[b] Some hunt units had specific numbers of permits for specific areas in the hunt unit.

Table 47. Elk trend counts and calf and bull per 100 cows ratios for the Sand Creek elk herd in Idaho, 1980-1988 (Parker et al. 1983, Chu et al. 1989a).

Year	Calves/ 100 cows	Bulls/ 100 cows	Trend count
1980-81	50a	23	2,310
1981-82	50	25	2,327
1982-83	65	18	2,959
1983-84	53	20	1,803
1984-85	44	18	2,553
1985-86	60	19	2,269
1986-87	46	20	682b
1987-88	54	33	2,815
1988-89	--	--	2,441c

a Calf ratios for 1980-81 and 1981-82 were assumed to be 50 and the bull ratios are calculated from this assumption.

b No trend count was conducted and this number represents the total number of elk classified for calculating calf and bull ratios.

c A comprehensive survey as not done. The trend count equals the minimum number of elk from random observations and ground counts at feeding sites.

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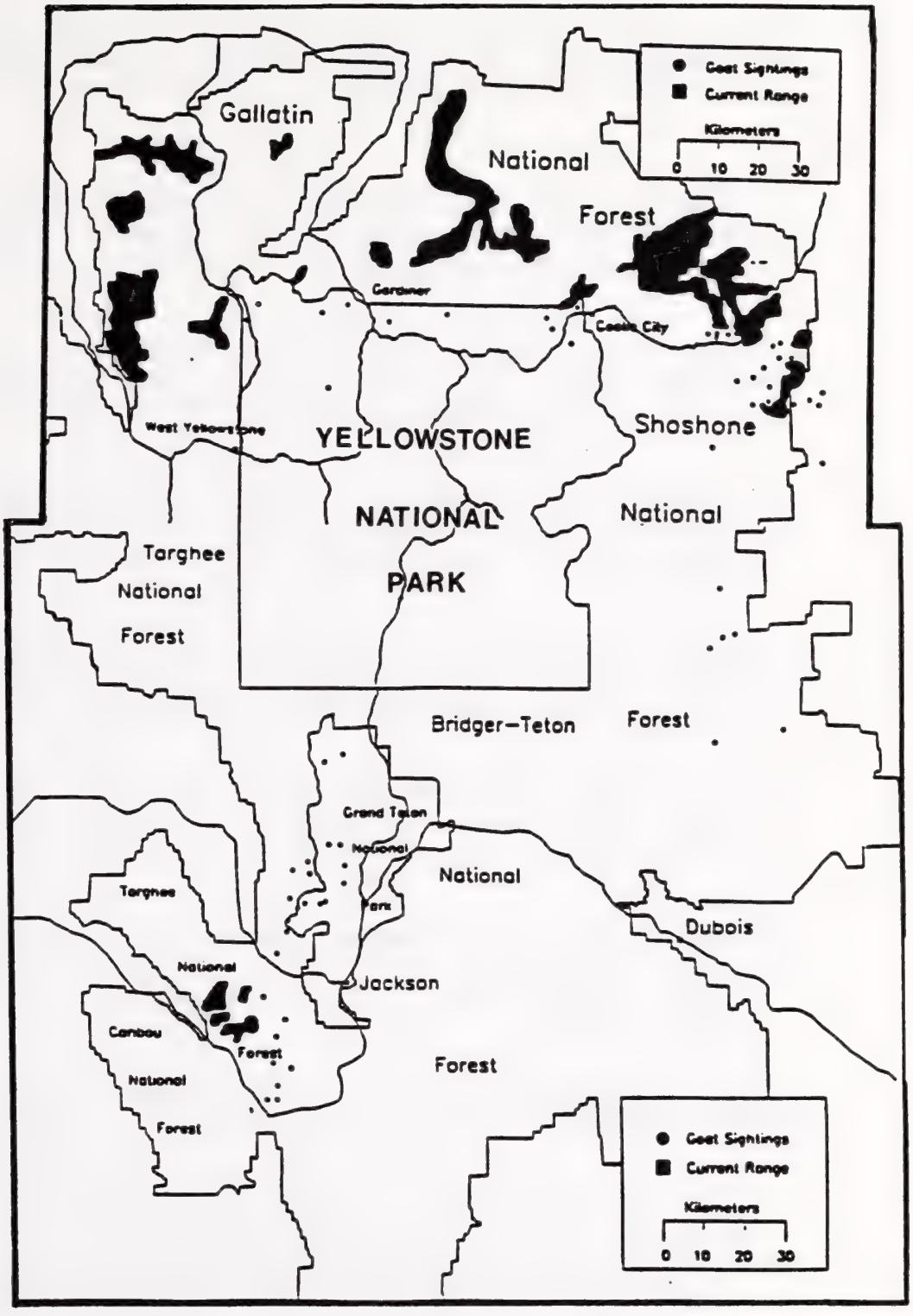
Table 48. Mule deer trend counts and fawn and buck per 100 does ratios for the Junipers winter range in Idaho, 1980-1989 (Kuck et al. 1989).

Year	Fawns/ 100 does	Bucks/ 100 does	Trend count
1980-81	92	65	---
1981-82	116	61	---
1982-83	---	--	1,443
1983-84	---	--	1,337
1984-85	72	32	1,983
1985-86	96	29	1,547
1986-87	121	37	---
1987-88	105	23	---
1988-89	83	42	1,684

Table 49. Moose classifications and twinning rates in Idaho (Region 6), adjacent to southwestern Yellowstone National Park, 1969-1988 (Ritchie 1978, Trent et al. 1984, Chu et al. 1988a).

Year	Calves/ 100 cows	Bulls/ 100 cows	Total Classified	Percent Twinning
1969	61	66	236	12
1970	65	96	125	10
1971	58	95	237	15
1972	56	70	138	17
1973	62	48	248	9
1974	85	61	113	15
1975	59	71	233	7
1978	64	100	71	--
1979	86	109	69	--
1980	100	200	--	--
1983	56	112	100	--
1984	93	---	76	--
1985	58	44	73	--
1986	50	111	47	--
1988	56	48	213	--



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STUDY AREA AND METHODS

The study area consisted of the 100,000-ha winter range of the northern Yellowstone elk herd. Houston (1982) described this area in great detail and summarized the information gathered prior to 1980 on the elk herd and its winter range. This elk population is probably the most studied elk population in North America. Houston's excellent monograph identified key factors in the dynamics of this population and provided a basis for projecting population changes in the future.

Wolves have been the subject of an enormous amount of research in North America and Eurasia (Tucker 1988); however, most of this research has been directed at wolf populations preying upon moose (Alces alces) and white-tailed deer (Odocoileus virginianus). Only a few studies have concentrated on wolves preying upon elk (Carbyn 1974, 1983; Scott and Shackleton 1980; Ream et al. 1986). Recent efforts to integrate and synthesize information on wolves throughout their range (Keith 1983, Fuller 1989) suggested that information from populations preying upon a variety of ungulate species can be combined to produce a cogent description of wolf population dynamics. Attempts have been made to evaluate relationships in terms of universal characteristics such as prey weight and density so information from a variety of species can be combined. This analysis relies heavily upon the extensive research and publications of key researchers such as D. Mech, L. Carbyn, and F. Messier. Their field studies and insights form the basis for the quantitative models developed here.

Our basic approach was to 1) identify key relationships in the dynamics of the northern Yellowstone elk population, 2) identify interactions of wolves with their ungulate prey and 3) gather quantitative information from the literature to model the relationships statistically. All analyses were performed on the Statistical Analysis System (SAS Institute 1985) running on an IBM PS/2 Model P70. The relationships were then incorporated into a computer simulation written in Turbo Pascal 5.0 (ELK WOLF MODEL - instructions for operation are available from the National Park Service, Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190). This model was used to project the results of various scenarios for restoring gray wolves to the greater Yellowstone ecosystem. It was used to identify the key relationships and the sensitivity of the outcome to these key relationships.

Our approach consisted of three parts: 1) a review and analysis of information summarized in Houston's (1982) monograph and of National Park Service data gathered since 1979 (Singer 1988, Singer et al. 1989), 2) an analysis of published information on wolves preying on ungulates throughout North America, and 3) a synthesis of these relationships into the simulation model. Each part will be described in order.

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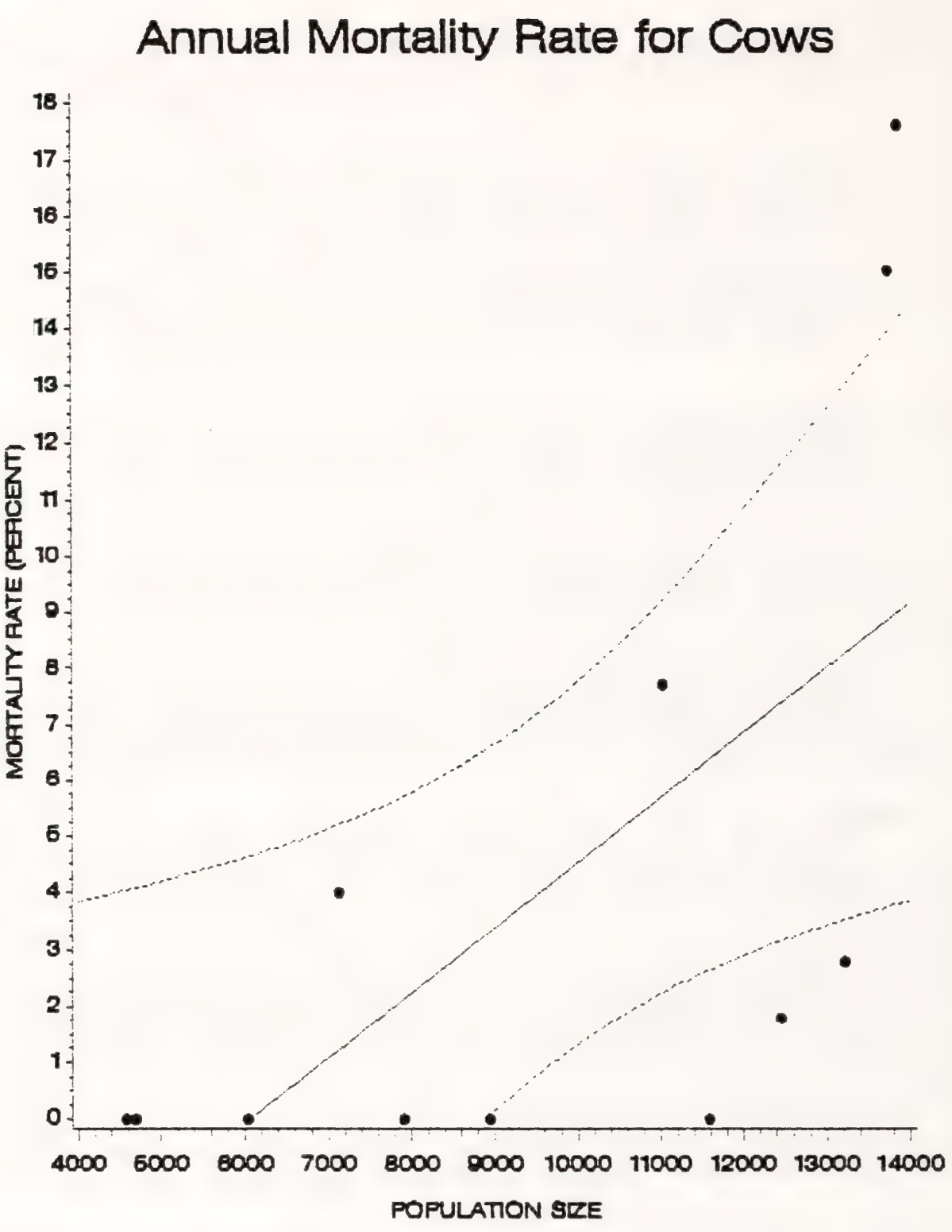


Fig. 1. Relationship between pre-harvest population size and annual mortality rate for cows.

DISTRIBUTION OF BEAVER IN YELLOWSTONE NATIONAL PARK 1988-1989

Susan L. Consolo and Donay D. Hanson
U. S. Department of Interior
National Park Service
Division of Resource Management
P.O. Box 168
Yellowstone National Park, WY 82190

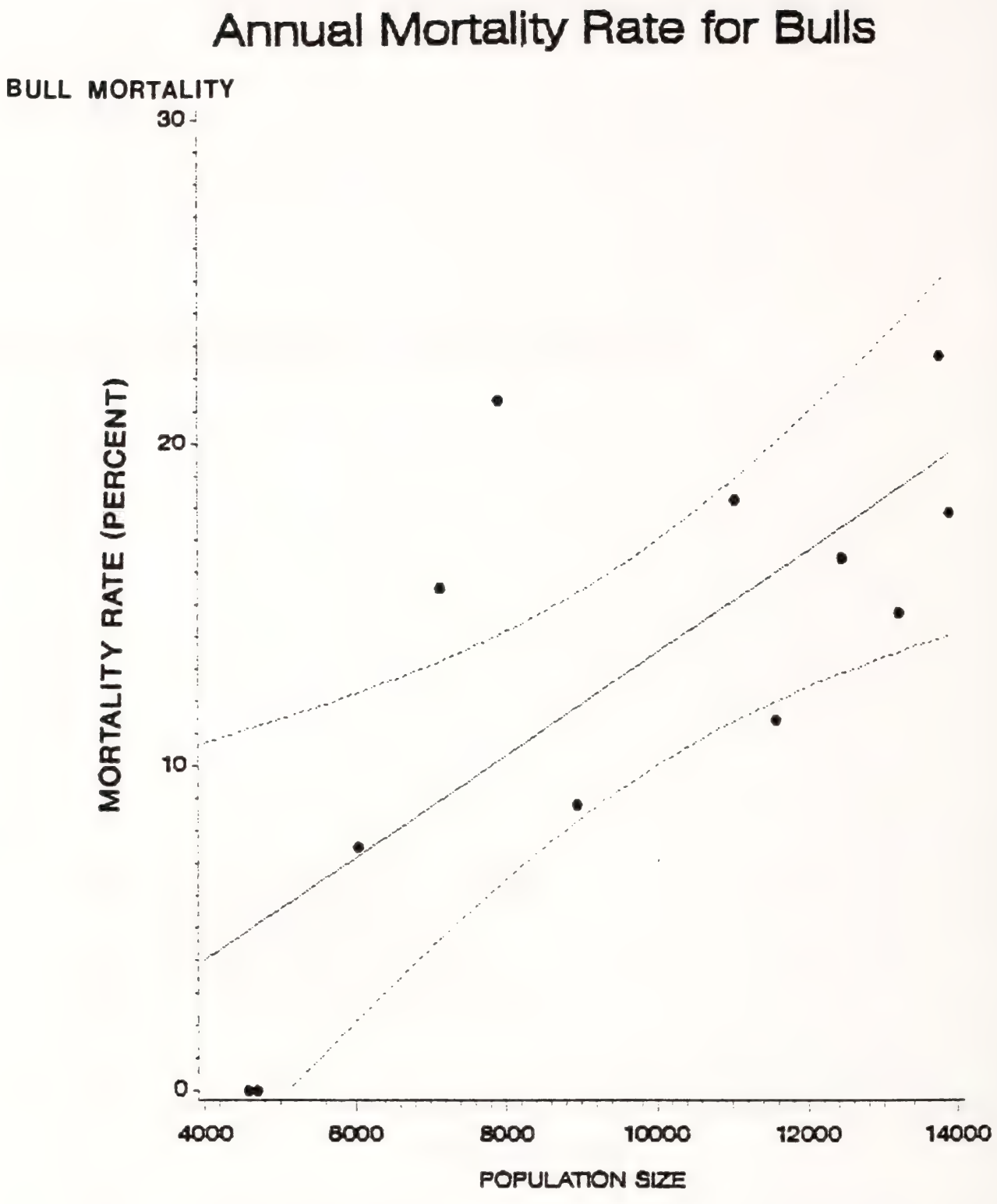


Fig. 3. Relationship between pre-harvest population size and annual mortality rate for bulls.

CURRENT DISTRIBUTION OF BEAVER IN YELLOWSTONE NATIONAL PARK

Susan L. Consolo and Donay D. Hanson, National Park Service,
Resource Management and Visitor Protection, P.O. Box 168,
Yellowstone National Park, WY 82190

EXECUTIVE SUMMARY

1. Much of Yellowstone National Park is marginal beaver (Castor canadensis) habitat, but beaver have persisted here since the park's inception.

2. In 1988-1989, 460 km (285 miles) of riparian habitat in Yellowstone National Park was surveyed to determine current presence and distribution of beaver. Forty-three stream segments or lakes had signs of current beaver activity, and 42 reliable observations of at least 27 individual beavers were collected.

3. Beaver are expected to be a secondary prey item if wolves (Canis lupus) return to Yellowstone; however, they could be vulnerable to the effects of predation in portions of the park where they are sparsely distributed.

4. More information and work is needed on the following: 1) levels of beaver trapping and poaching along park boundaries; 2) comparisons of historic records of beaver with trends in climate, hydrology, and riparian vegetation; and 3) development of a long-term monitoring program for beaver presence and abundance in Yellowstone National Park.

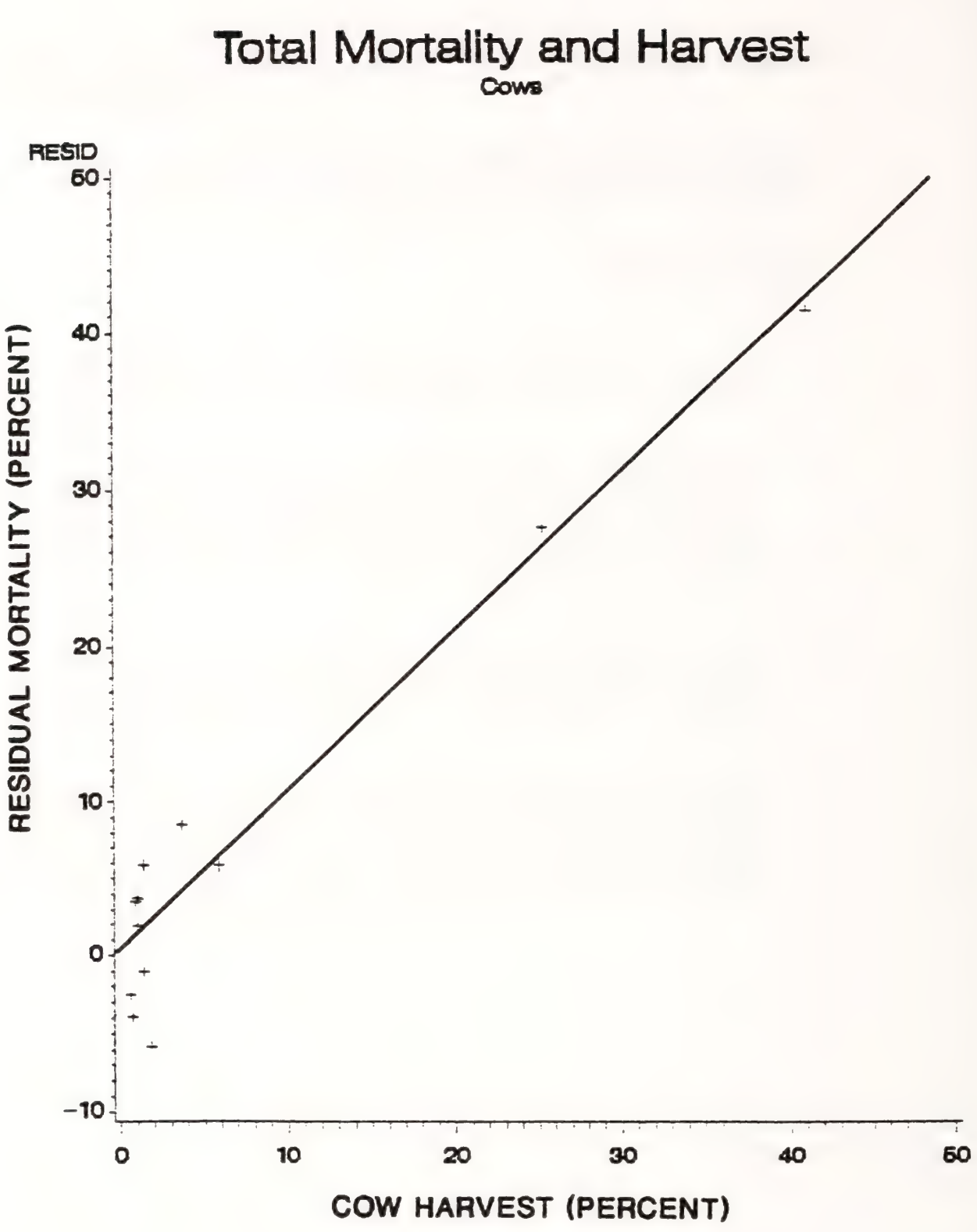


Fig. 5. Plot of the residuals after removing effects of population size and winter severity from the regression model of total mortality of cows.

DISTRIBUTION OF BEAVER IN YELLOWSTONE NATIONAL PARK, 1988-1989

Susan L. Consolo and Donay D. Hanson, National Park Service, Resource Management, P.O. Box 168, Yellowstone National Park, WY 82190

ABSTRACT: In 1988-1989, 460 km of riparian habitat (streamside and wetland areas) in Yellowstone National Park was surveyed to determine current presence and distribution of beaver (Castor canadensis). Forty-two reliable observations of at least 27 individual beaver were collected during the survey. Forty-three active stream segments or lakes with current signs of beaver activity, 82 sites with signs of previous activity, and at least 26 stream segments or lakes with both present and previous activity were identified. A total of 140 lodges were located; half (71) of these were thought to be active. This updated baseline information may be used by other researchers investigating riparian systems and in predicting potential effects of wolves (Canis lupus) on prey species. River segments and pond sites monitoring should continue on a cyclic basis to periodically assess the status of beaver in Yellowstone.

Relatively little monitoring or research has been done on beaver (Castor canadensis) in Yellowstone National Park. In the earliest days of the park's history, Park Naturalist M. P. Skinner made notes on the beaver. The first detailed study of Yellowstone Park beaver and their workings was done in 1921 and 1923 (Warren 1926). That study concentrated on the northern portion of the park, particularly in the Yancey's Hole region (Tower) near the Yellowstone River. Warren concluded in his summary report that beaver were overstocked in Yellowstone and that available aspen (Populus tremuloides) were being destroyed faster than they were being replaced in accessible areas. In 1953 and 1954, Jonas (1955) studied beaver in the park, in the "Camp Roosevelt" region near Tower, and collected some information from more widespread drainages throughout the park. He concluded that the beaver population was highly unstable, in a state of flux, and that these conditions had existed for 30 to 40 years. He attributed this largely to a lack of preferred foods due to 1) marginal habitat and xeric (dry) conditions, 2) the overpopulation of beaver in the 1920's mentioned by Warren, and 3) the overpopulation of elk (Cervus elaphus) in the 1950's.

From 1970 to 1979, ungulate-vegetation relationships were studied on Yellowstone's northern range (Houston 1982). Houston noted that beaver occurred throughout the northern range in the 1970's, but that most colonies in the park appeared to be ephemeral and that the "available evidence does not support earlier interpretations of competitive exclusion of beaver by elk" (Houston 1982:183). Fullerton (1980) surveyed beaver sites to establish current baseline information and speculated on patterns of colony persistence and turnover. She noted apparently persistent colonies in seven areas that varied from stream courses a few miles in length to extensive riparian regions encompassing major portions of townships.

In 1986, the park intensified its efforts to understand the ecology of Yellowstone's northern range with part of this program focusing on riparian zones, including the status of beaver. The scientific community has expressed

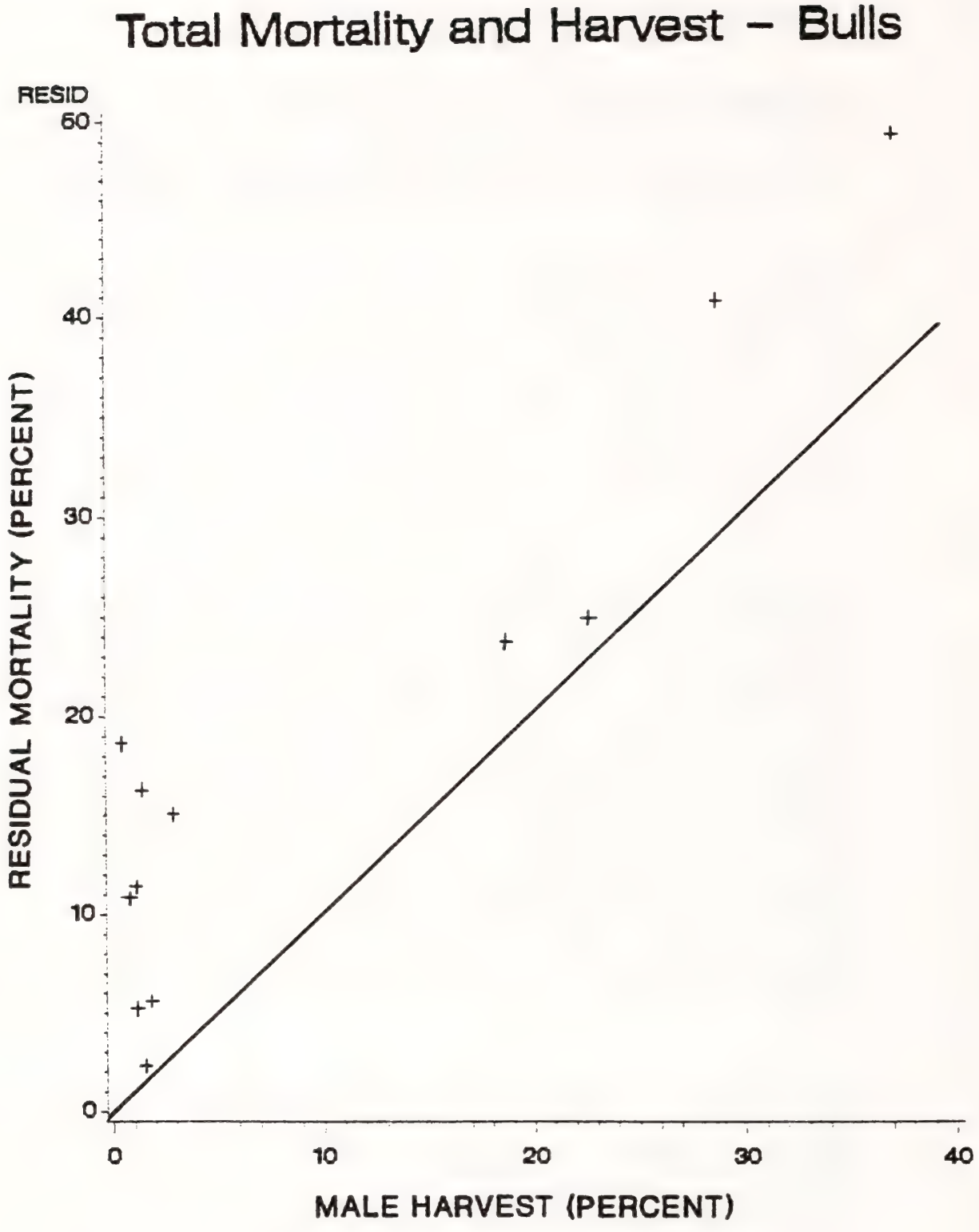


Fig. 7. Plot of the residuals after removing the effects of population size and winter severity from the regression model of total mortality of bulls.

(1982) estimated aspen covered 1,400 ha or between 2% and 3% of the northern range. Aspen also occurs in small acreages on the western and southern edges of the park. Despain (1975) listed 20 species of willow occurring in Yellowstone. Mountain alder (Alnus incana) and black cottonwood (Populus angustifolia) also occur in the park and are often associated with beaver. Approximately 36% of the park burned to some degree in the summer of 1988 (Despain et al. 1989).

Five major river basins drain the park (Fig. 1). The Yellowstone River drains the eastern half of the park. From its source in Wyoming's Teton Wilderness, the upper Yellowstone meanders through the Thorofare region in the park's southeast corner. Between the park's southern border and the Southeast Arm of Yellowstone Lake is approximately 23 km of river valley averaging 1.5 km wide. The gradient is nearly level, and the river is bounded by tall willows. Numerous ponds exist, and nine tributaries flow into the upper Yellowstone. Where the Yellowstone River flows into Yellowstone Lake it forms a broad, marshy delta with extensive willow and cottonwood communities. Yellowstone Lake occupies 4% of the park, covering 35,400 ha at an average depth of 42 m. It has 124 known tributaries; few have documented beaver activity in recent years (R. Gresswell, U.S. Fish and Wildl. Serv., pers. comm.). The river flows northward out of Yellowstone Lake at Fishing Bridge. It passes through the sagebrush/grassland of Hayden Valley in the central portion of Yellowstone, then drops over two waterfalls in the Grand Canyon of the Yellowstone River. Here the character of the river and its riparian zone changes considerably as it continues northward around the Washburn Range and into the lower elevations of the park. The Lamar River and several other major tributaries drain from higher ridges and plateaus into this stretch which bisects the park's northern ungulate winter range. Another major tributary, the Gardner River, joins the Yellowstone at the town of Gardiner, Montana, on the park's northern boundary. The Gardner and its tributaries drain the east side of the Gallatin Range.

The Madison River and its tributaries drain the west-central portion of the park, including the Central and Madison Plateaus and the geyser basins in the Firehole Valley. Much of this area is dry lodgepole forest, punctuated by thermal features. Except for the lower 6.5 km of the Madison River Valley, there are no noticeable communities of willows, cottonwoods, or aspen in these riparian zones. The Gallatin River drains the west side of the Gallatin Mountain Range in the northwest corner of the park. Along the park border, the riparian zone contains substantial areas of willow, grass, and sagebrush on a mild gradient.

Natality

Pregnancy rates were modeled with multiple regressions on population size the previous winter and on winter severity as developed by Houston (1982:238). These regressions were used for yearlings, two-year-olds, and prime-age females. Pregnancy of oldest-age females appeared to be independent of density and winter conditions.

WOLF POPULATION DYNAMICS AND FEEDING

Keith (1983) and Fuller (1989) summarized information on population characteristics of wolves. They demonstrated that increases in the prey population can cause wolf densities to increase and wolf territory size to decrease. They also demonstrated a relationship between prey abundance per wolf and characteristics such as pups per pack, percent pups, and the rate of population change (lambda). A similar approach was taken and a similar index based on the weight of prey per wolf in metric tons was developed. These relationships were incorporated into a Markov matrix model of population dynamics (Crabtree 1988). The model treats social classes rather than age classes. The wolf population is broken into three social classes: pups (young of the year), alphas (dominant pack members), and betas (subdominant, nonbreeding helpers). Nonpack members (loners and dispersers) were not included in the current model, but they will be included in the final model. In the present model, it was assumed that wolves entered the population as pups and that survivors became betas as yearlings. Betas could survive to the following year as betas or could become alphas. Animals that left the pack were considered mortalities. Alphas either survived as alphas or died.

Pup Recruitment

Fuller (1989) showed a highly significant relationship between the number of pups per pack and the index of prey per wolf. A regression of pups per pack on prey weight per wolf was used (Fig. 9).

Survival Rates

Based on a small amount of data, evidence was found that the survival rate of dominant pack members increased as more prey became available per wolf (Fig. 10). In contrast, the probability of a beta remaining a beta decreased with increasing prey per wolf ratios (Fig. 10). This did not occur because mortality was increasing; rather, the likelihood of a beta becoming an alpha increased through dispersal and pair formation, resulting in a decline in the number of betas remaining as betas in subsequent years.

The southwest corner of Yellowstone receives the largest average annual amount of snowfall in the park and retains much of that moisture in wet meadows until late summer. The Falls River and its major tributaries, the Bechler River and Boundary Creek, drain the Madison and Pitchstone Plateaus and flow out of the park into southeastern Idaho. The Bechler Meadows are characterized by a mixture of grassland, wet meadows of tufted hairgrass (Deschampsia caespitosa), sedges (Carex spp.), and isolated stands of conifers. Aspen is present but not abundant. The rivers are lined by substantial willow communities with occasional alder present. The Lewis and Snake Rivers which flow south into Teton National Park drain the south-central portion of Yellowstone Park. The Lewis River drains Lewis and Shoshone Lakes and the Pitchstone, Madison, and Central Plateaus. The Snake River drains the Red Mountains and Two Ocean Plateau. Valleys formed by these topographical features contain occasional willow and aspen communities within a high elevation coniferous forest.

METHODS

Using information from recent, known beaver observations and from previous beaver surveys, routes were identified along lakes and stream segments to survey in 1988-1989. The park maintains a file of wildlife observations dating back to the 1940's or earlier, although the observation cards for beaver apparently disappeared from the files in 1986. Thus, we relied on information from experienced park staff and other seasoned observers to reconstruct reference points of recent beaver activity and sightings. These were prioritized based on our preliminary assessment of known available beaver habitat. In August 1989, two aerial surveys were conducted, lasting approximately four hours each, to identify potential habitat and areas for ground survey. Surveys took place on 15 August, 1989, (eastern half of the park) and on 29 August, 1989, (western half of the park). The upper Yellowstone was surveyed during both flights. Active areas were positively identified by green leaves on beaver dams or lodges, although bank dens, caches in rivers, and some other signs of activity were undoubtedly not observed. Large lodges were easily seen, although whether lodges were active could not be accurately determined. Based on all available information, 84 lakes or stream segments were identified and prioritized for survey.

Ground survey methods involved walking or horseback riding along stream courses and examining pond or lake sites known or reported to have beaver activity in the past or present or that appeared to have suitable habitat characteristics. The lower 3 km of the Yellowstone River delta was surveyed from a canoe. As time permitted, lodges and dams were monitored in the early morning and evening hours to observe beaver and determine present activity. Activity, classified as present, recent, or old, was documented on field data sheets. Present/recent activity was noted on topographic maps and later computerized using UTM (Universal Transverse Mercator) coordinates (Fig. 2). Present activity was identified by obviously fresh cuttings, wood chips, shoots with green leaves, or fresh mud on lodges and dams. Recent activity was indicated by no positive sign of activity during the survey year; activity was estimated to be between 1 and 5 years old. Old activity was characterized by obvious abandonment of the site, indicated by collapsed beaver lodges, grayed tree stumps or cut logs, and barely evident or long-breached dams. Active areas that also showed signs of old activity were recorded as sites with long-term beaver presence.

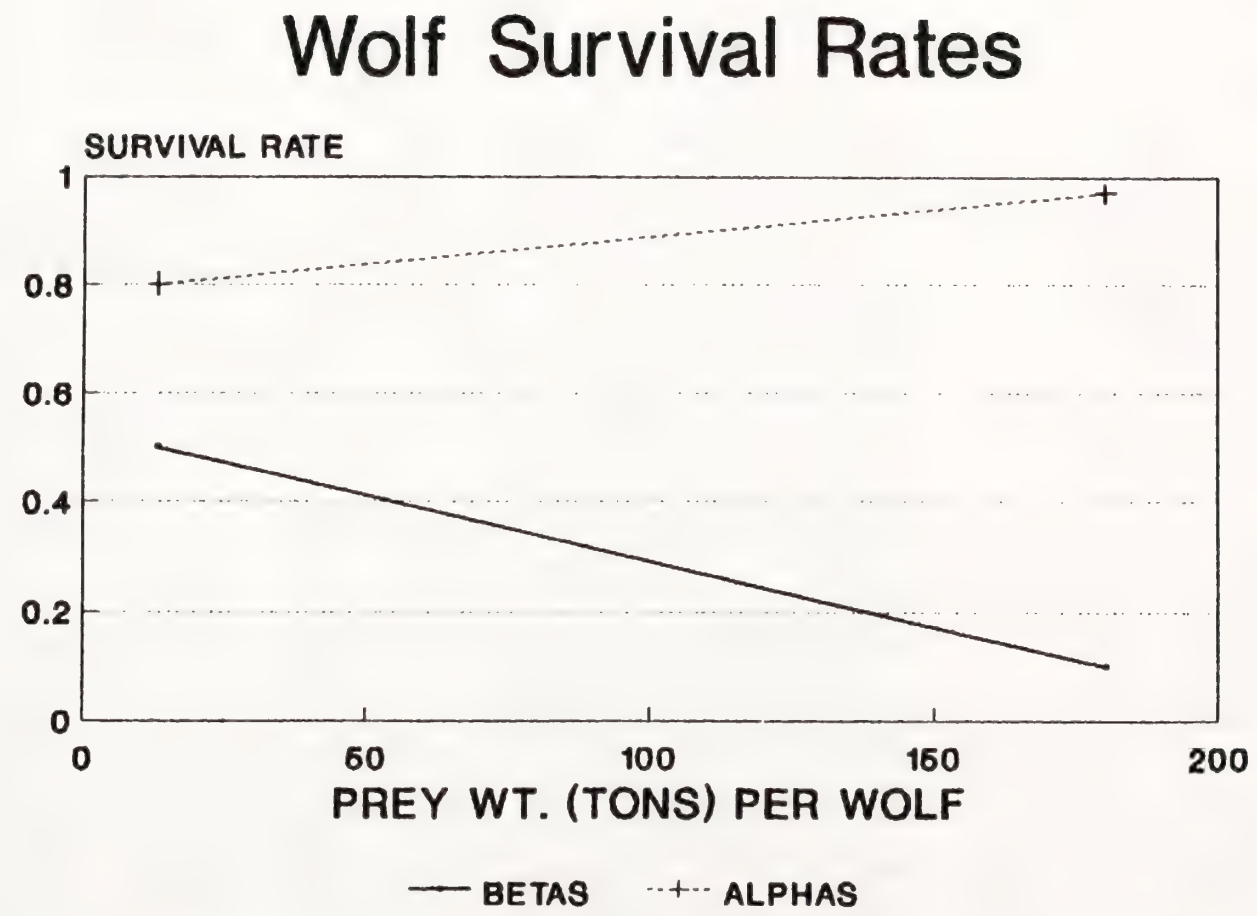


Fig. 10. Relationship between survival rates of pack members and prey available per wolf.

RESULTS

During the survey, 42 reliable beaver sightings were reported throughout the park (Fig. 2). These sightings represented a minimum of 27 individual beavers. Between May and October of 1988 and 1989, a two-person crew hiked or rode roughly 990 km to survey 460 km of riparian habitat (Table 1). Eight stretches of river, 5 km or longer, and 107 sites were surveyed (Fig. 1), representing 88% of the 84 targeted survey routes. The remaining routes were not completed due to time and weather constraints. Forty-three currently active sites or areas, 82 sites or areas with signs of previous activity, and 26 stream segments and lakes with signs of both present and previous activity were identified. A total of 140 lodges were located; half (71) of these were thought to be active, 8 were characterized as recently abandoned (1-5 years ago), and 61 were thought to be occupied by beaver more than 5 years ago. Three river segments had signs of both present and previous activity continuously for at least 5 km.

Other signs of current activity, such as dams, canals, fresh caches, wood chips, and beaver tracks, were documented. These were grouped geographically into areas that contained active sign. Thus, a complex of ponds with five dams and a single large pond formed by one dam were each recorded as one area of activity. There were 71 areas of past and present activity that included dams; 29 looked active, 8 appeared to be recent, and 34 were obviously very old. As found in other areas (Easter-Pilcher 1987), not all beaver colonies build dams. Of the 43 locales with current signs of beaver activity, only 29 areas had active dams. Most of these were on small creeks (<3 m wide) and rivulets, such as those running into the Gallatin and Lewis Rivers. Larger creeks and rivers had very few dams, though numerous lodges, caches, bank dens, and other signs were found. This is not surprising on such fast-moving streams as the Snake River and Slough Creek, which typify many park rivers that have substantial water level fluctuations between spring runoff and winter freeze-up.

DISCUSSION

Signs of numerous persistent beaver colonies typified by abundant lodges, caches, cuttings, and dams were found in the upper Yellowstone River/Thorofare region, the Bechler region, the lower elevation reaches of the Gallatin River drainage, and portions of the Madison River drainage near West Yellowstone, Montana. This is consistent with the findings of Fullerton (1980). Along the Bechler River and Boundary Creek, for example, approximately one active lodge per 0.8 km of river was found, and lodges not associated with dams or ponds were identified. Numerous ponds of the Gallatin and Madison drainages had several lodges and dams. Vigorous willow communities were present, and aspen or other hardwoods were present nearby. As expected, these areas were outside the park's predominant rhyolitic plateaus in broader, flat valleys. Each of these areas also receives considerable snowfall compared to the drier northern range along the lower Yellowstone River.

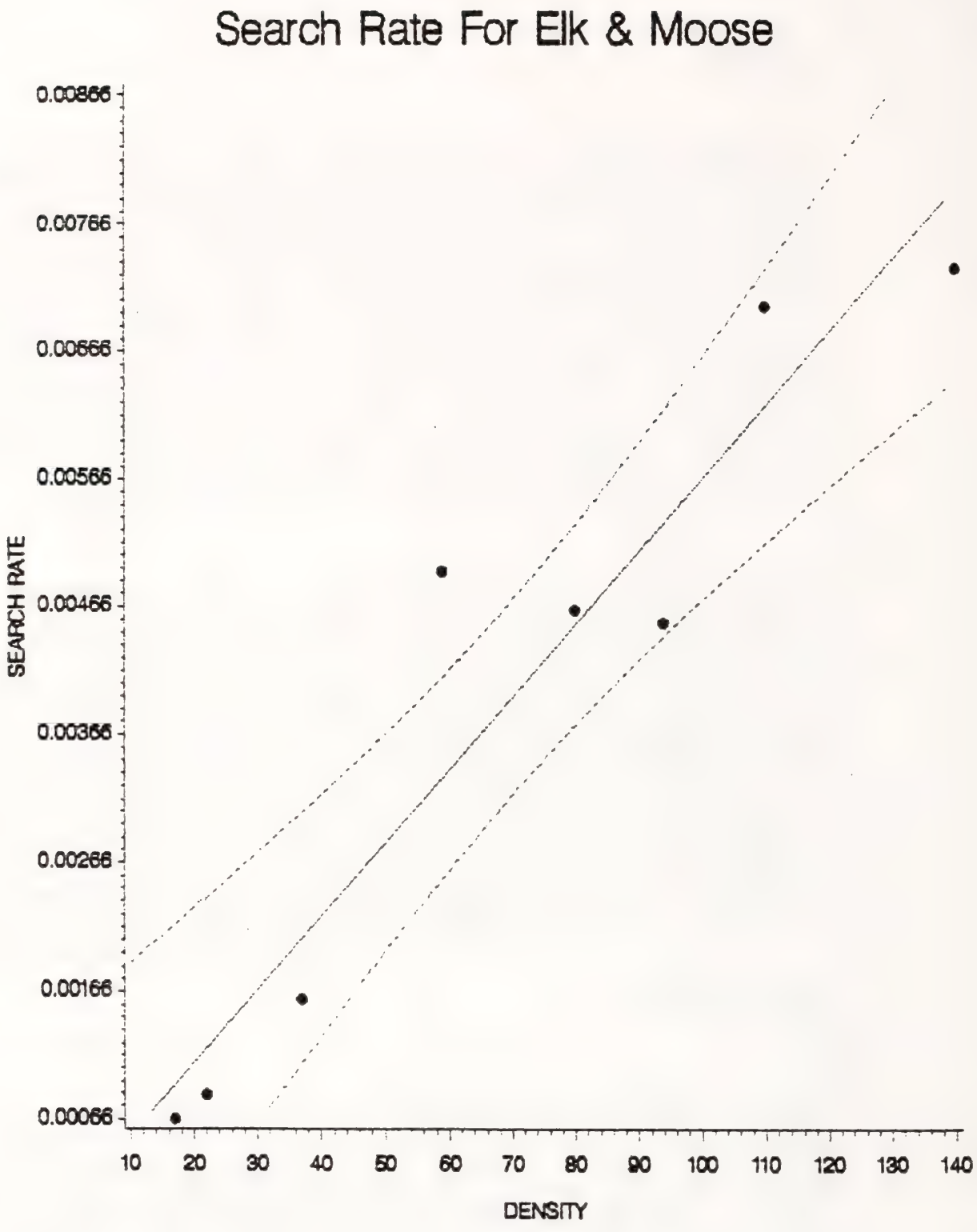


Fig. 11. Relationship between search rate and prey density for elk and moose.

built, and the flooding characteristics of the associated riparian zones. The overall impression gained from aerial observation was that old sign of beaver activity did not exceed the amount of current activity; rather, it appeared that old dams, lodges, and other signs remained visible for decades after abandonment as beaver moved from site to site.

During the ground surveys, beaver colonies were found in areas that appeared to offer suitable habitat, as expected. This did not necessarily require aspen, but beaver colonies with persistent activity in Yellowstone usually were associated either with sizable willow or aspen communities. In some sites, aquatic vegetation, such as the pond lily (Nuphar polysepalum), appeared to be the major food for beaver. We surveyed a few areas in which aspen was present but which beaver did not appear to use. There may have been more risk associated with leaving the cover adjacent to the watercourse in order to reach the aspen than the beaver found acceptable. However, in another survey area, beaver appeared to regularly cut and move aspen across a busy highway, despite the fact that they made themselves vulnerable to predators and vehicular traffic.

Some signs of beaver activity were undoubtedly missed, both in surveyed and unsurveyed locations. Particularly on large rivers not suited for beaver dams, some bank dens were observed, but others were likely unnoticed. Most importantly, the amount of beaver sign observed is not indicative of beaver numbers (Townsend 1953, Hay 1958, Swenson et al. 1983, Easter-Pilcher 1987); however, it does reflect current animal presence and distribution.

SUMMARY AND CONCLUSIONS

In 1988-1989, Yellowstone National Park can be characterized as having beaver active in approximately 43 sites or areas. These locations vary from single pond or lake sites to riparian zones along 5 km or more of one creek or river. At least 26 streams, lakes, or areas currently occupied by beaver show signs of long-term beaver presence. Seven sites or areas in the northwest, southwest, and southeast portions of the park are classified as high-quality beaver habitat. The sites are characterized by a permanent watercourse with low to moderate gradient, moderate seasonal water level fluctuation, and persistent aspen or willow communities as compared to the northern and central portions of the park. These sites are likely to be continuously occupied by beaver, although beaver may not be present in all areas of available habitat or in consistent densities over time.

Other sites vary in terms of the water regime and the nearby vegetative cover types and in their potential ability to support relatively stable versus ephemeral beaver colonies. Tributaries to the Snake River and the Yellowstone River north of the lake are mostly steep, rocky, and exhibit extreme water level fluctuations. On the Snake River, one recently active lodge was 2-3 m above the level of the river in mid-July. Such large fluctuations limit the size and persistence of beaver colonies (Retzer et al. 1956). Further research could enhance understanding of how beaver survive in these different types of habitat and determine the size of colonies in the different areas of the park.

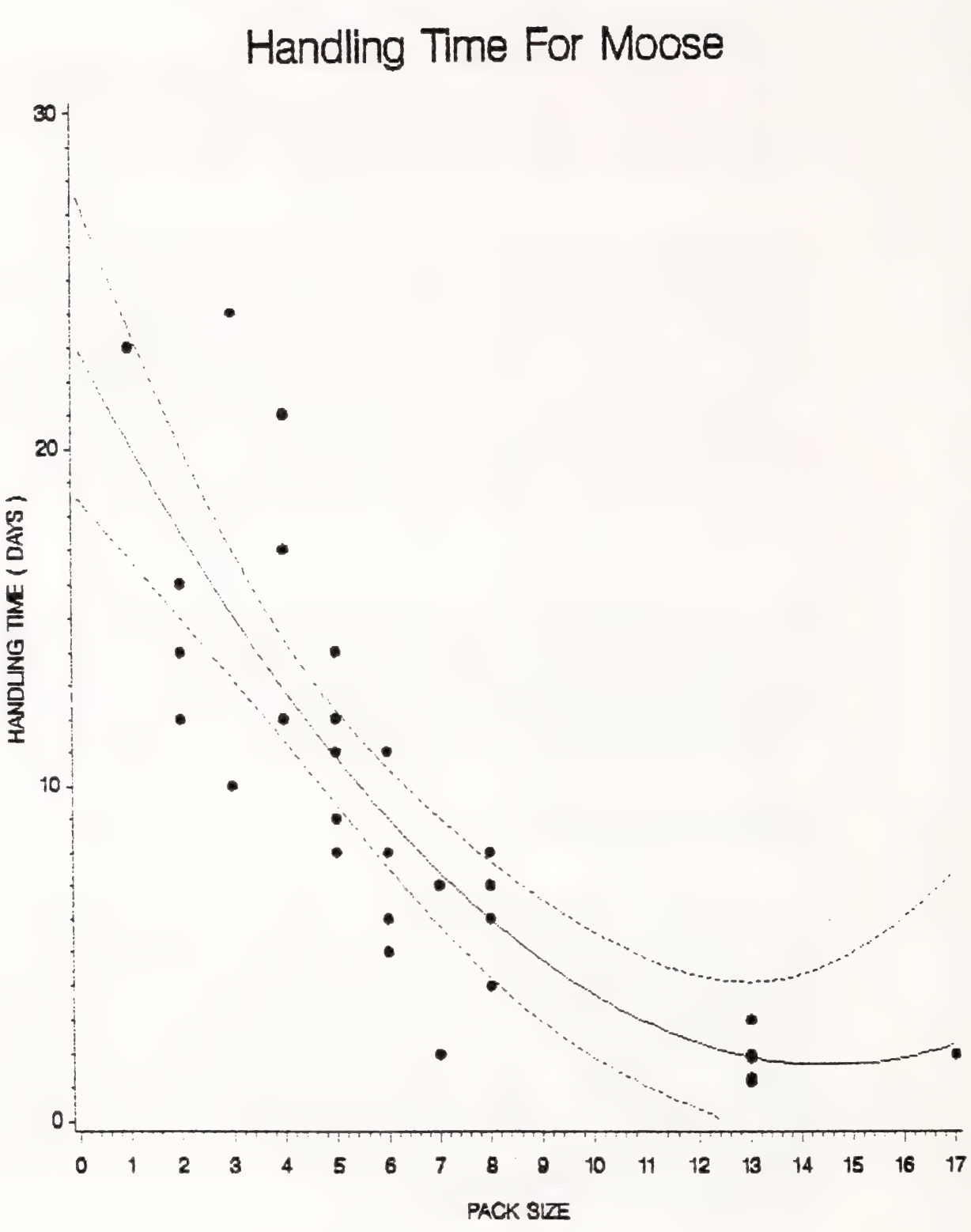


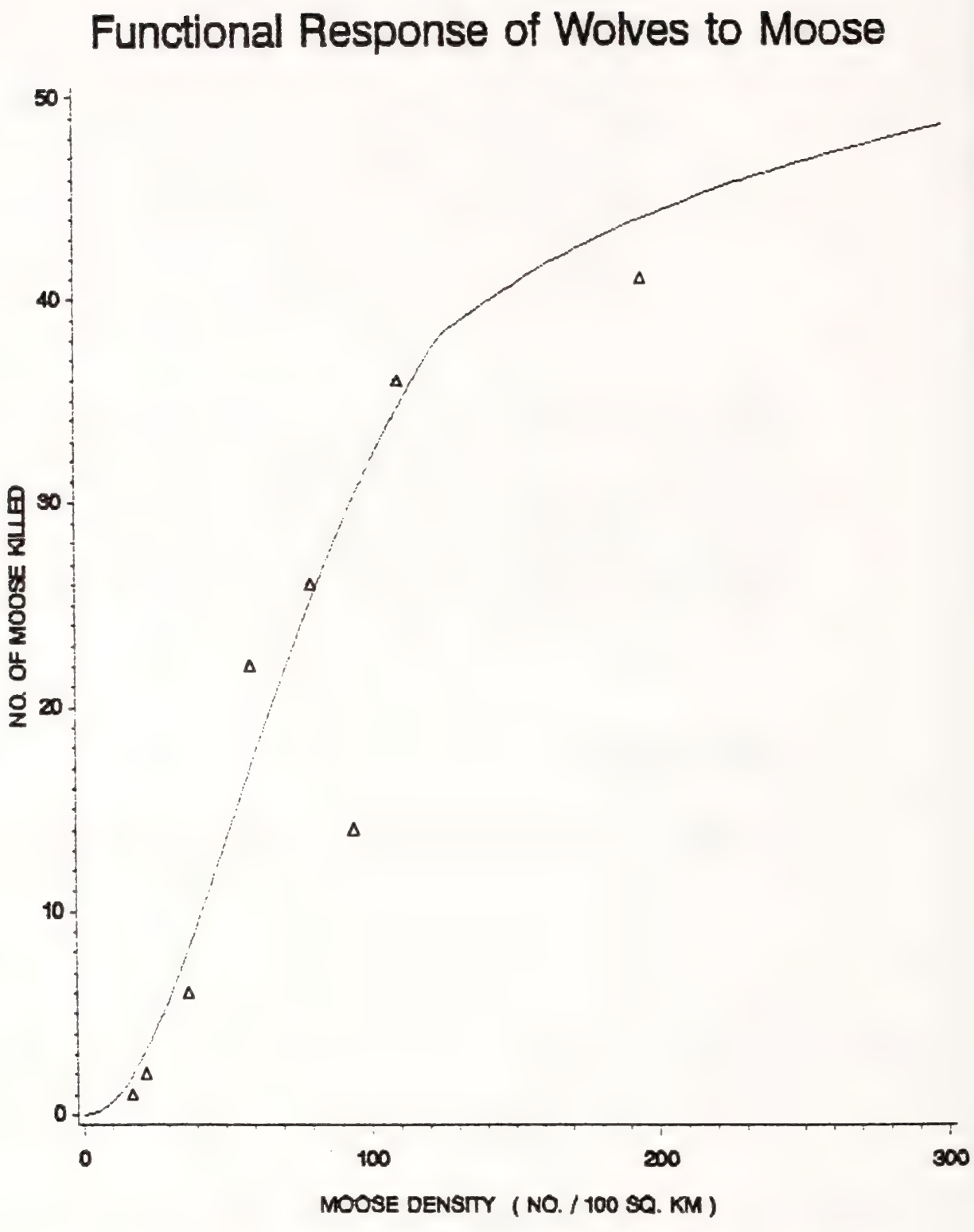
Fig. 13. Relationship between predator handling rate and predator pack size.

3) development of a regular beaver monitoring program in the park. At a minimum, aerial surveys should be done in September and October approximately every 5 years to identify areas of potential beaver activity. This is the only efficient way to find new activity in remote areas and to survey areas that are otherwise fairly inaccessible, such as the Yellowstone River delta. However, aerial surveys are not sufficient to determine current versus abandoned beaver sites. Rather, a cyclic monitoring scheme should be initiated where a percentage of survey areas with previous or potential beaver activity are surveyed on the ground each year with each area being revisited approximately once each decade. Eventually, monitoring routes should be prioritized incorporating information from a stream classification or habitat classification system.

Beaver were observed in sufficient numbers and distribution to indicate that, other site influences remaining equal, they are in no imminent danger of extinction in Yellowstone National Park. Beaver along the western and southern borders should not be vulnerable to wolf predation; however, beaver on the northern range and in other areas may be vulnerable due to their low densities. Efforts to increase incidental observations of this (and other) species will continue. There are plans to eventually record all present and historic beaver observation and activity records into a geographic information system to maintain a long-term data base.

ACKNOWLEDGEMENTS

M. Meagher and G. Bowser assisted in planning and organizing the survey methods. J. and E. Caslick helped review and edit the manuscript.



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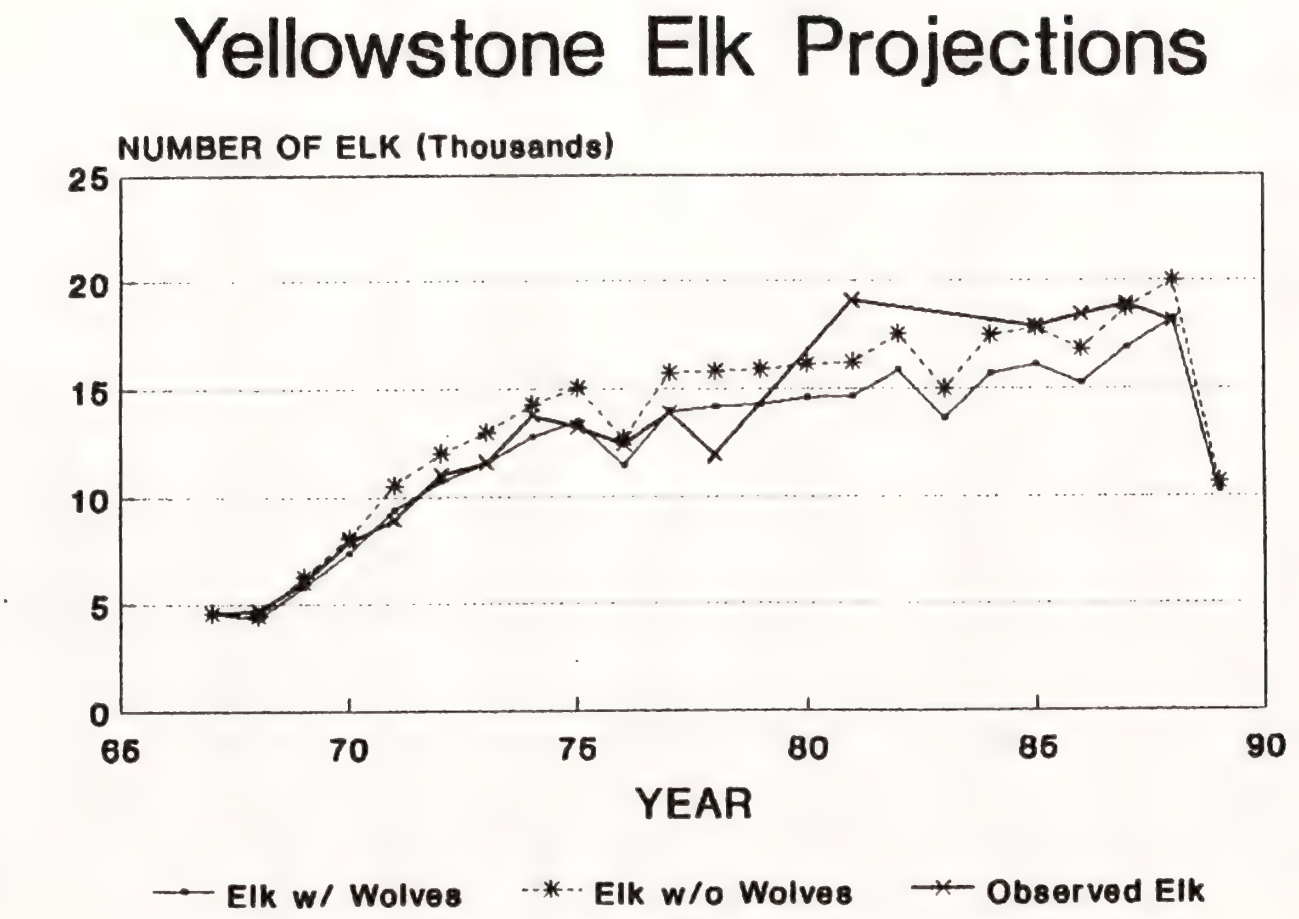

Fig. 16. Model projections of changes in elk numbers under different scenarios.

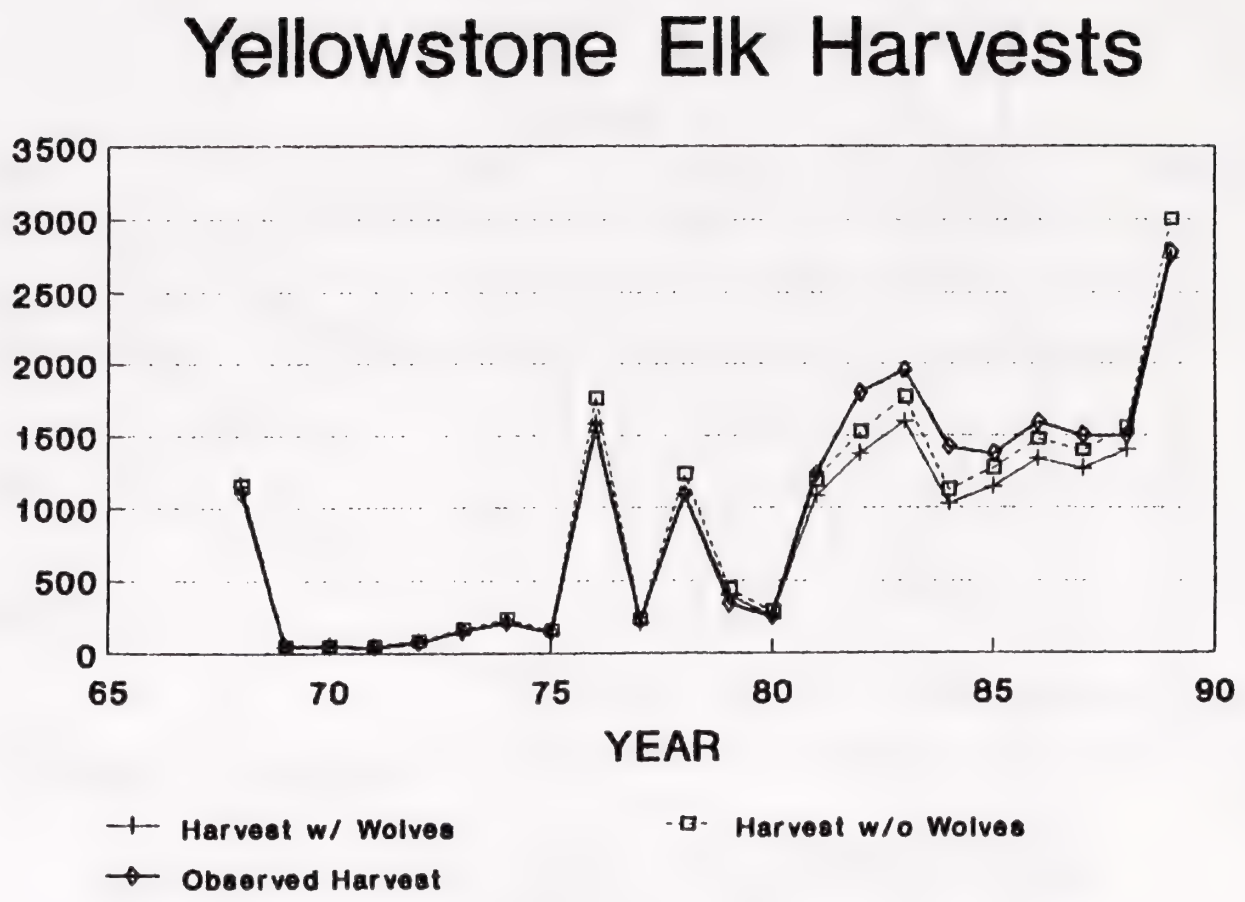

Fig. 17. Model projection of changes in elk harvests.

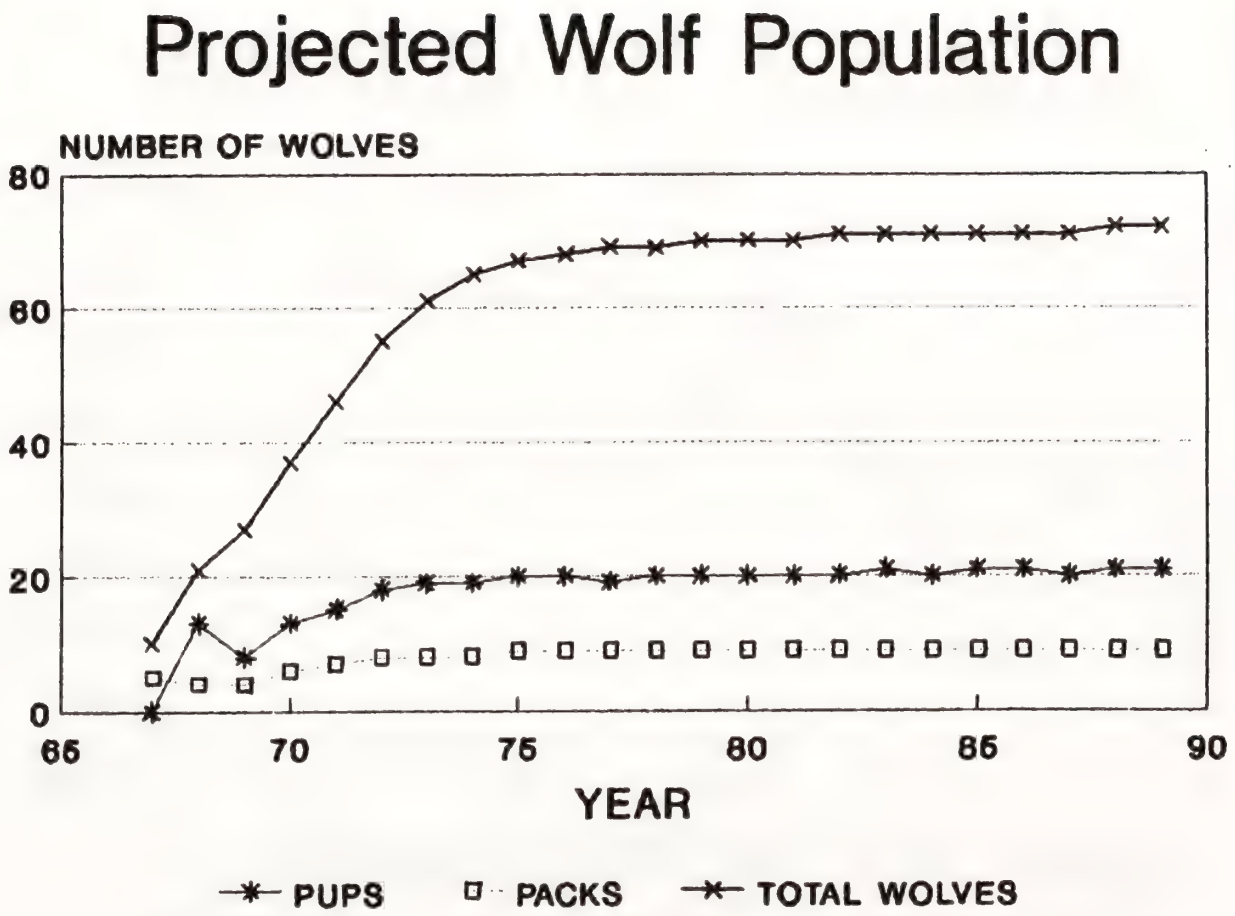

Fig. 18. Model of projected growth in the wolf population.

Wolf Impacts on Elk

The model predicted that the wolves would kill in excess of 1,000 elk per winter when both populations were at their peak. Under this scenario, about 1,500 elk per winter would be removed from the population, but the elk seemed able to maintain their numbers indefinitely under this level of predation (Fig. 16). The level of hunter harvest decreased slightly, but the change was relatively minor (Fig. 17).

CONCLUSION

The extensive information available concerning population dynamics of the northern Yellowstone elk herd allowed us to make fairly precise predictions of population size given annual information on winter severity, winter range size, fire effects, and hunter harvest. Using information gleaned from the literature concerning wolf population dynamics and feeding behavior, reasonable but less certain predictions about the future of combined elk and wolf populations were made. These projections implied that the northern range could support at least nine packs, totalling approximately 75 animals. The elk population would decrease somewhat, but the decrease would not exceed 10% under the conditions modeled. Future work will incorporate the effects of snow conditions on wolf predation success, incorporate loners and dispersing wolves into the models, and model the populations of bighorn sheep, bison, moose, mule deer, and pronghorn (Antilocapra americana) occupying the same winter range. Information on species other than elk is much more limited, which places constraints on what can be discerned. The potential effects of wolf predation on other predators, on sport hunting, and in surrounding areas will be evaluated in detail. Finally, these analyses will be extended to the Clarks Fork elk herd.

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ESTIMATES OF THE POTENTIAL INTERACTIONS BETWEEN HUNTER HARVEST AND WOLF PREDATION ON THE SAND CREEK, IDAHO, AND GALLATIN, MONTANA, ELK POPULATIONS

David J. Vales and James M. Peek
University of Idaho
Department of Fish and Wildlife Resources
Moscow, ID 83843

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David J. Vales and James M. Peek, University of Idaho
Department of Fish and Wildlife Resources, Moscow, ID 83843

EXECUTIVE SUMMARY

1. Estimates of the potential effects of gray wolf (Canis lupus) predation on the Gallatin, Montana, elk (Cervus elaphus) herd, and the Sand Creek, Idaho, elk herd are presented. These populations occupy Yellowstone National Park for a portion of the year, and are hunted when they occur outside of the park in fall and winter. Special hunts for both herds are used to control populations and prevent damage by elk on their winter ranges. We assumed that hunter harvest was accurately measured for these populations, and concluded that both population sizes are underestimated.

2. In the Gallatin elk herd, we estimated that up to 10 adult wolves could be supported at current elk population levels if hunter harvest were reduced from the 1983-1985 average of 436 elk to 300-400 elk, if harvest were restricted primarily to bulls, and if elk constituted between 75% and 90% of the wolf diet. If five wolves were present, harvest rates on antlerless (cow or calf) elk could be sustained at approximately half the current estimated level and produce a hunter harvest ranging from 350 to 450. This assumes no change from current population size. A compensatory response in the form of a 5% increase in survival of all sex/age classes of elk was of insufficient magnitude to change these conclusions.

3. If wolf predation on the Sand Creek population is confined to elk using Yellowstone National Park for 150 days, a hunter harvest of between 170 and 270 elk could be sustained on this population segment if ten wolves were present, but only by reducing cow harvest and increasing bull harvest. This harvest is similar to the 1980-1988 average of 219 elk. If wolves were allowed outside of southwest Yellowstone National Park, hunter harvest of Sand Creek elk could range from 640 to 770 with ten wolves on this population segment, a slight reduction from the 1980-1988 average of 738.

4. Our investigations suggested that heavily hunted elk populations can support wolves only if hunting pressure is directed primarily at bulls. We also believe these elk populations are larger than estimated, if the estimated harvest levels are reasonably accurate. It should be obvious that both predator and prey will have to be more intensively monitored than at present if both hunters and wolves are to occur together. Potential compensatory responses between the mortality factors and survival will be a major area for study if wolves again occupy this region.

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ESTIMATES OF THE POTENTIAL INTERACTIONS BETWEEN HUNTER HARVEST AND WOLF PREDATION ON THE SAND CREEK, IDAHO, AND GALLATIN, MONTANA, ELK POPULATIONS

David J. Vales, Department of Fish and Wildlife Resources,
University of Idaho, Moscow, ID 83843

James M. Peek, Department of Fish and Wildlife Resources,
University of Idaho, Moscow, ID 83843

ABSTRACT: Two models were used to project the potential effects that gray wolf (Canis lupus) predation would have on the Gallatin, Montana and Sand Creek, Idaho elk (Cervus elaphus) herds. Models were used to estimate current population size, survival, fecundity, and composition from available data. The sizes of model populations were determined to be larger than reported in state agency progress reports in order to support the observed hunter harvest. A range of wolf predation rates were then applied to the model populations and effects on population size and potential hunter harvest were evaluated.

The Gallatin elk herd size was estimated to be between 1,800 and 2,500 elk in winter. With year-round wolf predation equally distributed across all population segments, average total hunter harvest would decline from the 1983-1985 average of 436 to between 300 and 400 in the presence of five wolves, with no change in elk survival or reproductive rates. Reducing the cow harvest to half of the 1983-1985 average levels would be required to maintain a stable elk population. The Sand Creek elk herd was estimated at 4,300 elk in winter. If wolves are restricted to within the boundaries of Yellowstone National Park, and wolves prey on migratory Sand Creek elk only during summer, the estimated average hunter harvest of 219 elk between 1980 and 1988 could be maintained by decreasing cow harvest and increasing bull harvest with no change in elk survival or reproductive rates. If wolves are tolerated outside of Yellowstone National Park, and wolves prey on migratory elk on y during summer and fall, hunter harvest would decline slightly from the 1980-1988 estimated ave age of 738 elk to between 640 and 770 with 10 wolves. Both elk herds require special hunts to harves migratory segments from Yellowstone National Park in order to keep populations within manageme it goals. Wolf predation could potentially compensate for this harvest. It is recommended that intensive monitoring of both predator and prey populations be done if wolves are restored to Yellowstone National Park.

Key words: elk, Gallatin, modeling, predation, Sand Creek, wolves

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INTRODUCTION

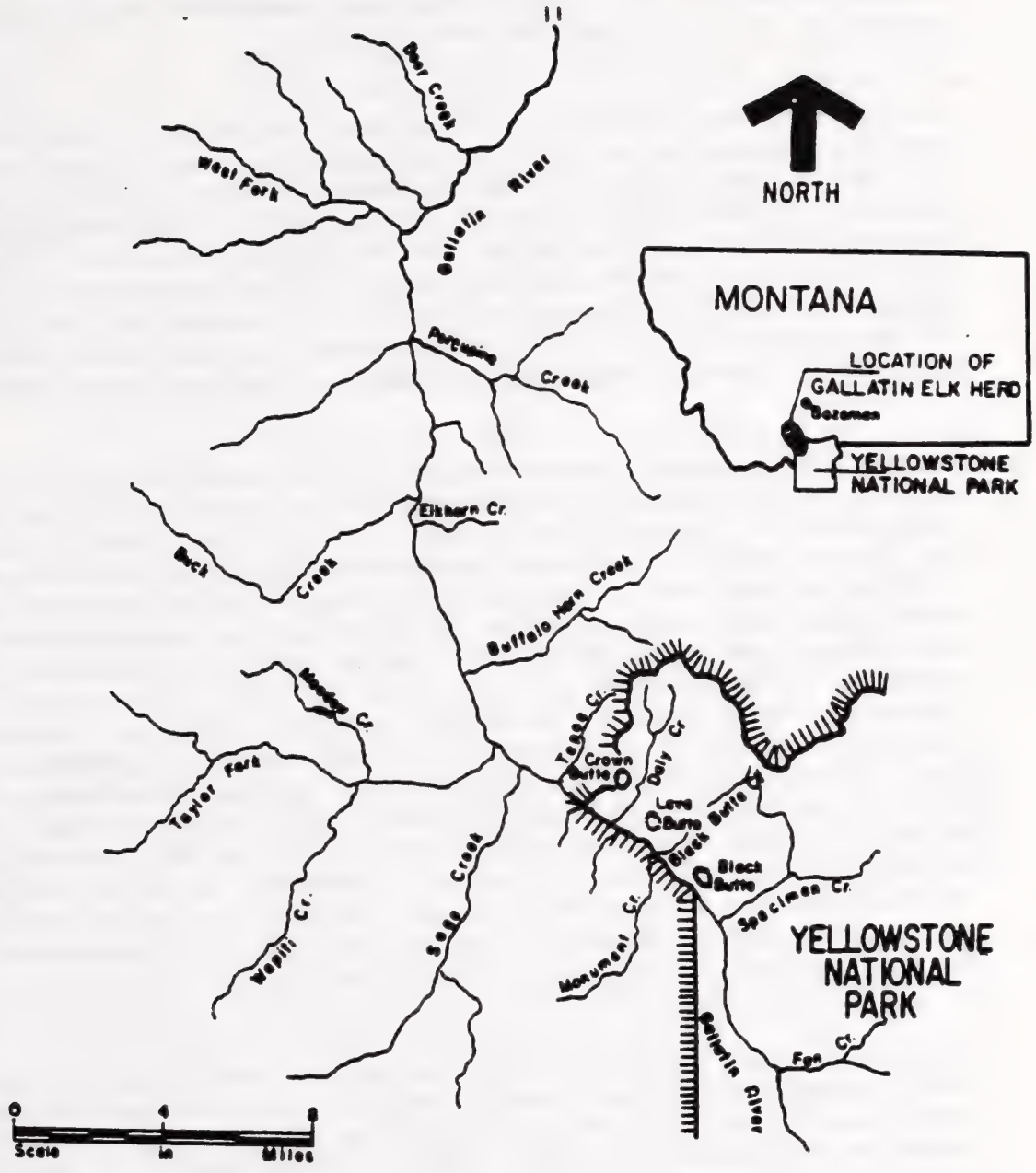
The potential for gray wolf (Canis lupus) restoration in Yellowstone National Park (U.S. Fish & Wildlife Service 1987) raises the question of what effect this species may have on the prey base, particularly elk (Cervus elaphus) populations. Two elk populations, the Gallatin herd in the northwestern portion of the park and the Sand Creek herd in the southwestern portion of the park, are subject to hunting when they migrate beyond park boundaries. The purpose of this study is to provide a preliminary assessment of the potential effects of wolves on these elk populations, estimate the size of wolf populations that could be supported by the prey base, and estimate the number of elk available for hunters, should wolves be restored to the area.

This study was supported by the National Park Service, Yellowstone National Park, and the College of Forestry, Wildlife and Range Sciences, University of Idaho. We thank Francis Singer and John Varley of the Research Office at Yellowstone National Park for their patience and encouragement. Justin Naderman, Idaho Department of Fish and Game, provided helpful comments on the Sand Creek elk, moose, and deer populations. Steve Fritts, U.S. Fish and Wildlife Service, Wayne Brewster, Norm Bishop, and Francis Singer, National Park Service, provided comments on the manuscript.

GALLATIN

Elk and Other Ungulate Populations

The following species occupy the Gallatin area (Fig. 1): elk, bighorn sheep (Ovis canadensis), mule deer (Odocoileus hemionus), moose (Alces alces), mountain goats (Oreamnos americanus), and beaver (Castor canadensis). These big game species are hunted when they occupy habitats in Montana along the Gallatin River. Information on these species was obtained from Taylor (1982-1986). Populations of bighorn and mountain goats are relatively low, and will not be important in the wolf diet. Mule deer, moose, and beaver may provide part of the wolf diet. There are no population records for beaver, but harvest records are available for mule deer and moose. An average of 85 mule deer (range 71-100) were taken from the upper Gallatin Hunting Unit 310 from 1980 to 1986; most of these were from the Taylor Fork and Porcupine Creek drainages, farthest from Yellowstone National Park. An average of 21 moose (range 15-30) were harvested during permit hunts between 1980 and 1986 in the upper Gallatin, of which 15 (range 11-26) were bulls. The moose harvest is reasonably well distributed across the hunting unit. We concentrated here on the effects of wolf predation on the elk population because elk are expected to be the primary prey (Koth et al. 1990). There is not enough information to project effects upon other potential prey species, although we recognize that they may become an important part of the wolf diet.



GALLATIN ELK WINTER RANGE

Fig. 1. Map of the Gallatin elk herd winter range.

The upper Gallatin elk population in Hunting Unit 310 has nonmigratory and migratory segments. The primary winter range is along the northern boundary of the park and at lower elevations along the Gallatin River and its tributaries north to the West Fork. One segment moves into the Madison River drainage to winter in Hunting Unit 360 on the Bear Creek Game Range and adjacent lands, including the Beaverhead National Forest.

Nonmigratory elk are distributed within the Gallatin River drainage outside of the park, summering at higher elevations above the winter ranges. An average of 190 animals (range 77-320) have been harvested annually from this population between 1978 and 1985 (Table 1). From 1983 to 1985, the general harvest averaged 214 elk, including a permitted antlerless hunt. Permits were distributed through the hunting season to reduce harvest of resident elk and emphasize harvest of migratory elk in the vicinity of the park toward the end of the season. About 41% of this harvest has come from Buffalo Horn Creek and Sage Creek, the two drainages closest to the park, since 1981.

The migratory segment summers south of the winter range, at higher elevations both inside and adjacent to Yellowstone National Park. The migratory population is typically not subject to significant hunter harvest until after the general October-November season ends. Special late season harvests based on drawings are used to maintain the population at desired levels. A quota is established each year based on the prior winter survey, mortality and recruitment estimates (Table 1). Estimated carrying capacity of the winter range was 1,400 to 1,600 elk from 1978 to 1985. This number should allow vegetative conditions on the winter ranges to improve. Vegetative cover on permanent transects established on winter range has generally increased during the 1962-1985 period. Prehunting season population estimates range from 1,746 to 2,269 animals (average 2,070) over the 1978-1985 period. The population appears to have increased slightly from 1979 to 1985, concomitant with a decreasing trend in cow:calf ratios. Observed percentage of adult bulls ir this population changed from 10% in 1978-1979 to 20% in 1980-1982 to 15% ir more recent years, suggesting the age and sex distribution of males is fluctuating and the population is not stable.

Typically, 1,200 to 1,750 either sex permits are issued for hunts beginning in mid-December and lasting through January. The late season hunts from 1978 to 1985 averaged 246 elk (range 134-361) or 43% (20%-75%) of the quota, and comprised 48% (26%-69%) of the total known mortality. A decline in adult bulls resulted in changing the traditional either-sex permit hunt to one emphasizing antlerless harvest in 1984. Approximately 60% of the hunters drawing permits participated in the hunt.

Table 1. Determination of late season harvest quota for the Gallatin elk herd

	Year							
	1978	1979	1980	1981	1982	1983	1984	1985
Winter survey:								
Gallatin	1043	808	1245	1142	1450	1150	1125	1200
Madison	672	481	474	540	430	918	400	1097
Total counted	1715	1289	1719	1682	1880	2068	1525	2297
- YNP residents	100	50	150	200	430	500	-	500
- winter/road kill	100	53	70	50	25	60	-	60
- bulls[a]	152[b]	237[b]	300[b]	286[b]	285[b]	241	229	260
+ calf crop	750	560	588	585	445	494	583	532
+ bulls	152	237	300	286	286	241	229	260
- carrying capacity of winter range	1400	1400	1400	1400	1400	1400	1600	1600
Total	865	346	687	617	471	602	508	669
Quota	850	350	600	600	-	600	500	675
calf:cow ratio	55	59	49	51	39	39	45	36
Pre-hunting season Population estimate	2265	1746	2087	2017	-	2002	2108	2269
Elk removals								
General hunt	77	107	150	225	320	192	135	315
Late season hunt	248	263	134	361	296	317	211	136
Illegal kill	21	-	10	25	20	20	30	20
Winter kill	3	12	30	250	30	30	50	25
Road kill	19	7	20	40	30	30	25	30
Total removals	362	392	344	901	696	589	451	526

[a]1978-79 - 10% bulls, 1980-82 - 20% bulls, 1983-85 15% bulls.
[b]Calculated: not listed in state progress report.

A series of regression analyses of proportion of age classes in the late season harvests were used to assess possible trends in age structure of the harvest over the 1971-1984 period (Fig. 2). We found no trends in proportion of old, adult, three-, two-year old or yearling bulls or cows related to the size of the harvest (Table 2). However, there are trends related to year, suggesting that bulls 3 years old and adult cows have declined in numbers over the 16 year period (Table 2, Fig.2). Three-year-old bulls and cows, and old cows have appeared to increase. The declining trend in bull age structure is reflected in the observed decline in sex ratio (Table 1), which may also be reflected in the increasing number of old cows in the population. These analyses indicated that the population has been undergoing internal adjustments in age structure of both sexes, if the check station information reflects population trends. We decided to use the 1983-1984, 1984-1985, and 1985-1986 age structures from the general and late season hunts to calculate survival rates and population composition. This provided a sample of 1,110 ages from the three most recent years of information that were available.

For the Leslie matrix (Leslie 1945) projections, we smoothed the age structure of elk aged one year or older using log-linear regression (Caughley 1977:96). The proportion of animals in each age class was multiplied by the total prehunting population estimate of 2,500 to determine number of animals in that age class (Table 3). The old age class was assigned to specific ages 8-12, and the adult age class to specific ages 4-7 as indicated. We then applied this population, plus the total harvest of bulls, cows and calves to the Leslie matrix model and adjusted mortality, fecundity rates, and population size until a stable population representing the wintering herd was obtained. Fecundity rates specified that 50% of yearling females, 98% of adults aged 2-5, and 96% of older adults produce one calf each year. These rates are considered high. A harvest of 439 elk is obtained from this population, including 212 1+ bulls, 78 calves, and 148 1+ cows. The average harvest for the 1983-1984 through 1985-1986 years was 435, which included 209 bulls, 149 cows, and 69 calves.

A population with a finite rate of increase of 1.0001 was obtained when 50% of the bull and 13.5% of the cow and calf summer prehunt population was harvested. However, the actual population is obviously not this stable, since the estimated population size varied (Table 1). Comparison of the model and the age structure seen at check stations suggested that different proportions of the various sex and age classes from this population became available for harvest for the early and late seasons from year to year. These differences were due to changes in migration patterns, due to changes in hunting conditions that affected the vulnerability of the nonmigratory segment.

The Leslie matrix model indicated that a population size of 2,500 was necessary to maintain the observed harvest, and the sex and age composition of the herd. This estimate is approximately 300-500 elk higher than reported state agency estimates. We considered the harvest information to be the most reliable of all field data, and our model population estimates to be minimum estimates.

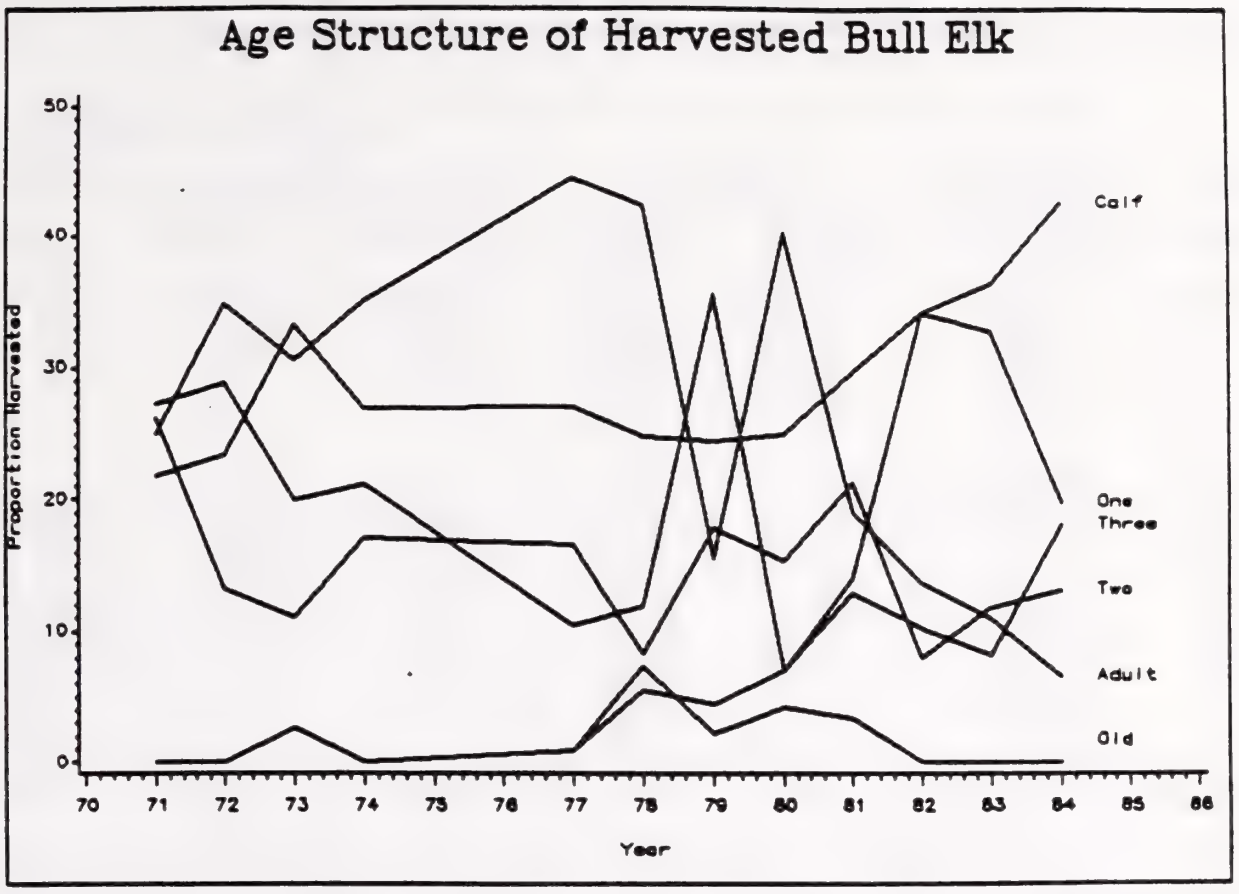


Fig. 2. Relationships between age structure of harvested bull and cow elk and year for the Gallatin elk herd.

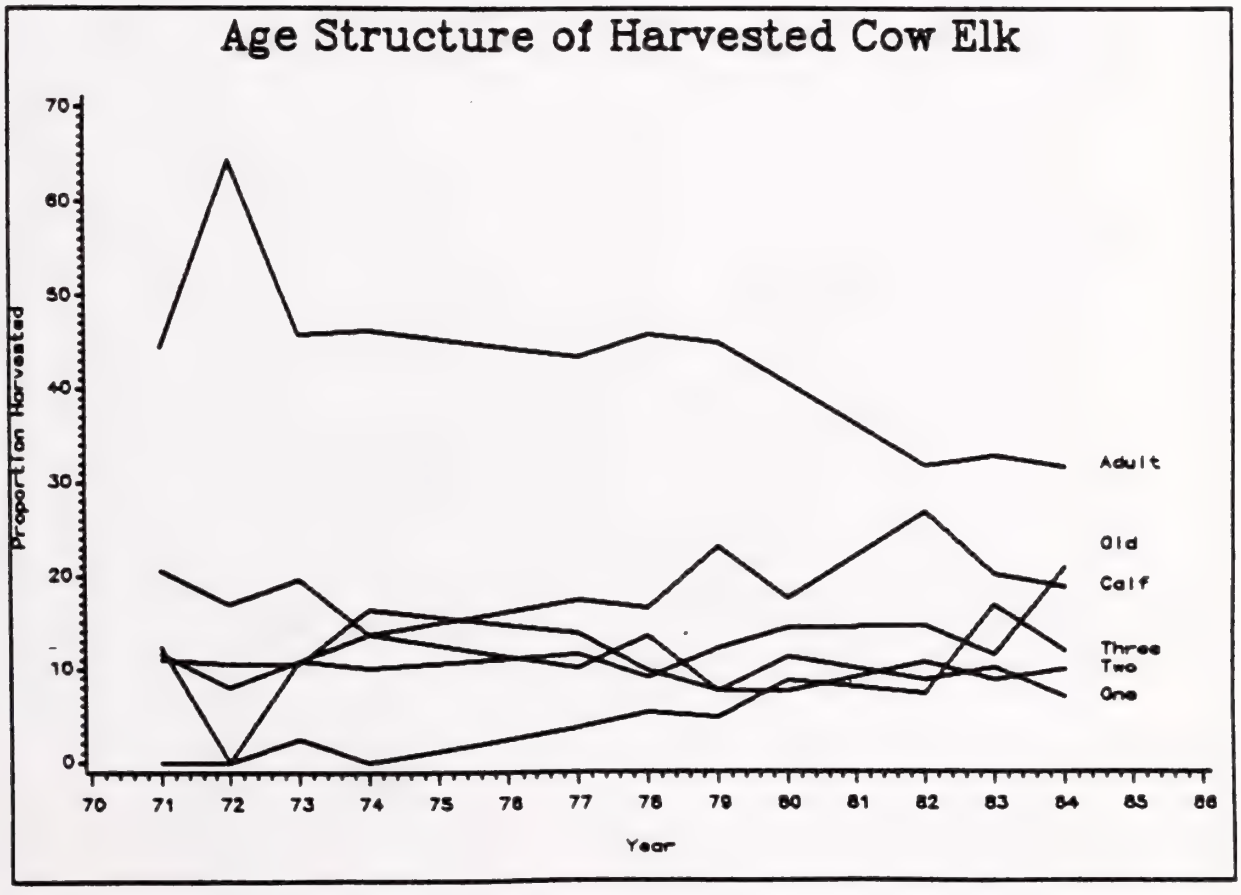


Table 2. Proportion of ages in Gallatin late season elk harvests by year and size of harvest: results of analysis of variance.

Sex-age	F	P	r^2	Regression coefficient if significant intercept	year	year*year
Bulls						
old	2.98	0.102	0.4	-2.40	1.75	-0.13
adult	8.86	0.008	0.66	22.61	5.74	-0.62
three	38.92	<0.001	0.8	-3.43	1.42	---
two	1.49	0.25	0.13	---	---	---
one	0.43	0.52	0.04	---	---	---
Cows						
old+adult	11.71	0.009	0.55	61.79	-0.122	---
old	6.95	0.027	0.44	5.65	0.98	---
adult	7.35	0.015	0.65	52.33	-0.44	-0.15
three	38.92	<0.001	0.81	-3.18	1.45	---
two	1.93	0.19	0.18	---	---	---
one	1.51	0.25	0.14	---	---	---
calf	1.11	0.32	0.11	---	---	---

Table 3. Estimation of fall age structures from hunter harvests for the Gallatin elk herd with population adjusted to 2498. Resident and migratory segments included.

	Check station 1983-1985		Smoothed		Adjusted to 2498[a]	
Age	Males	Females	Males	Females	Males	Females[b]
0.5	84	108	---	---	484	484
1.5	239	46	204	80	234	230
2.5	94	48	127	65	105	187
3.5	58	57	79	53	47	155
4.5	---	---	49	43	21	127
5.5	---	---	30	35	10	103
6.5(Adult)	(132)[c]	(160)	19	28	4	84
7.5	---	---	12	23	2	73
8.5	---	---	7	18	1	63
9.5(Old)	(11)	(73)	5	15	1	46
10.5	---	---	---	12	---	29
11.5	---	---	---	10	---	9
12.5	---	---	---	8	---	---
Total	618	492	532	390	909	1590

[a]Based on sex ratio of 21 bulls:100 cows and 51 calves:100 cows.
[b]Results of Leslie matrix model using mean harvest, sex and age structures from 1983, 1984, and 1985. Model run for 50 iterations.
[c]Check station aged as adult (4-7) or old (7+).

Discrete time step balance equations (Starfield and Bleloch 1986, Walters 1986, Eberhardt 1988) were used for the balance models. The models simply described the next year's population as a function of current population plus births minus deaths ($N_{t+1} = N_t$ + births - deaths). Accounting and model output are done at the end of the biological year prior to calving (referred to as spring population). Balance equation models used truncated age structures of three age classes: young-of-the-year, yearling, and 2-plus-year-olds. Truncating the age structure may affect the dynamics of the model by making it more sensitive to small changes in survival and harvest rates of adult age classes, especially females.

Population size and composition estimates were extracted from Montana progress reports (Taylor 1982-1986). For the population analyses, average estimates of population size, composition, and harvest between 1983 and 1985 (Table 1) were used in iterative models to obtain survival and fecundity rates that resulted in model populations having characteristics similar to real populations. Survival rates were partitioned to summer and winter seasons. For cases where the observed harvest could not be supported by the population estimated by state agencies, a larger population size was derived. In these cases, the population size modeled is the minimum size population that can support the average observed harvest and remain stable. Survival rates were high for these models. It is possible that the actual population size is larger and survival rates lower than modeled, however, lack of data prevented an accurate population estimate from being used.

Balance models were run iteratively until survival and fecundity rates were derived that gave a stable winter population of 1,600 with the observed average harvest of 436 (Table 4). Composition of the model population was 19 bulls:100 cows:50 calves in spring prior to calving. Yearling bulls were 63% of the bull segment, and yearling cows were 21% of the late spring, precalving female segment. Survival rates for the model population were 0.69 for calves, 0.88 for yearling cows, 0.90 for adult cows, 0.98 for yearling bulls and adult bulls. Survival rates were divided by season (Table 4). Bull survival and harvest rates are high, indicating that the model population should probably be larger than 1,600 to support the indicated harvest. A larger population would allow cow:calf ratios to drop to near the observed summer estimates of 100:40 (Table 1).

A second balance model was derived using an annual harvest of 407 elk from a spring population of 1,600 (Table 5). Composition of the population was 19 bulls:100 cows:45 calves in spring prior to calving. Yearling bulls were 57% of the bull segment, and yearling cows were 19% of the female segment prior to calving. Survival rates for the model population were 0.62 for calves, 0.89 for yearling cows, 0.92 for adult cows, and 0.94 for bulls. Again, survival rates appeared high, suggesting that the population size of the Gallatin elk herd in late winter prior to calving was greater than 1600 elk.

Table 4. Gallatin elk herd population characteristics: 1600 elk in late winter modeled for stability. Harvest of 436 is stable and constant from observed '83-86 average.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	242	397	306	272
yrl cows	199	242	235	219
2+ cows	770	969	940	826
M calves	242	397	306	272
yrl bulls	117	242	240	118
2+ bulls	70	187	185	69
Total	1640	2434	2212	1776
Composition				
bull:100 cow	19	35	36	18
calf:100 cow	50	66	52	52
yrl cow:100 2+ cow	26	25	25	27
yrl bull:100 2+ bull	167	129	130	171

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.77	0.90	0.69
yrl cows	0.97	0.91	0.88
2+ cows	0.97	0.93	0.90
M calves	0.77	0.90	0.69
yrl bulls	0.99	0.99	0.98
2+ bulls	0.99	0.99	0.98
Fecundity rates			
yrl cows	0.28		
2+ cows	0.96		

Harvest		Harvest rate
F calves	34	34/306 = 0.111
yrl cows	16	16/235 = 0.068
2+ cows	114	114/940 = 0.121
M calves	34	34/306 = 0.111
yrl bulls	122	122/240 = 0.508
2+ bulls	116	116/185 = 0.627
Total	436	

[a]Spring pre-calving is late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Table 5. Gallatin elk herd population characteristics: 1600 elk in late winter modeled for stability. Harvest of 407 is stable and constant from observed '83-86 average.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	221	411	292	258
yrl cows	185	221	217	210
2+ cows	802	987	967	853
M calves	221	411	292	258
yrl bulls	106	221	217	109
2+ bulls	80	186	182	81
Total	1615	2437	2167	1769
Composition				
bull:100 cow	19	34	34	18
calf:100 cow	45	68	49	49
yrl cow:100 2+ cow	23	22	22	24
yrl bull:100 2+ bull	133	119	119	135

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.71	0.87	0.62
yrl cows	0.98	0.91	0.89
2+ cows	0.98	0.94	0.92
M calves	0.71	0.87	0.62
yrl bulls	0.98	0.96	0.94
2+ bulls	0.98	0.97	0.94
Fecundity rates			
yrl cows	0.24		
2+ cows	0.97		

Harvest		Harvest rate
F calves	34	34/292 = 0.116
yrl cows	16	16/217 = 0.074
2+ cows	114	114/967 = 0.118
M calves	34	34/292 = 0.116
yrl bulls	108	108/217 = 0.498
2+ bulls	101	101/182 = 0.555
Total	407	

[a]Spring pre-calving is late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

The third balance model used a stable population size of 1,800 to maintain a harvest of 436 elk. (Table 6). A cow:calf ratio of 100:47 was still high. Survival rates for this population were 0.63 for calves, 0.89 for yearling cows, 0.90 for adult cows, and 0.93 for bulls (Table 6). The rationale for this model is that observed cow:calf ratios may be biased low.

The fourth balance model used a spring precalving population of 2,400 elk and a 436 harvest level (Table 7). The cow:calf ratio was 100:39 prior to calving. Survival rates were lower and appeared to be more realistic. The yearling:adult bull ratio was lower than previous models. No information was available on actual yearling bull:adult bull ratios, but the level of harvest of adult bulls probably has brought the ratio above equality. Within each model, as the sex ratio declined, the yearling:adult bull ratio increased. This ratio can be changed by using different survival rates for these two segments of the population.

Any one of these balance models or the Leslie matrix model might represent the actual population at one point in time. However, the conclusion that the elk population was larger than field estimates have indicated was supported by all analyses.

Wolf Predation

A summary of aspects of wolf predation applicable to this study was provided by Peek and Vales (1989), and is briefly reiterated here. Annual kill rates from 13 studies ranged 12 to 28 ungulates killed per wolf (Table 8). These estimates assumed that observed kill rates would be maintained throughout the year. The likelihood of reductions in kill rates in summer would be offset by the increase in calves in the kill, but these kill rates may prove to be high if alternative sources of prey become important.

During winter, mule deer populations in the upper Gallatin are primarily distributed away from the park, on the peripheries of the elk winter ranges. Assuming that wolves are most apt to be distributed in or close to the park, mule deer may not provide a major winter food source. Some mule deer would migrate during summer into and near Yellowstone National Park where they would be susceptible to wolf predation.

Moose populations are distributed across the upper Gallatin, with major wintering concentrations in drainages above the major elk winter ranges. Moose are therefore expected to be a more significant part of the wolf diet than mule deer. The probability is high that management actions and other human activities affecting wolves in this area will cause them to remain within Yellowstone National Park and the immediately adjacent periphery.

Table 6. Gallatin elk herd population characteristics: 1800 elk in late winter modeled for stability. Harvest of 436 is stable and constant from observed '83-86 average.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	253	455	332	298
yrl cows	211	253	245	229
2+ cows	875	1086	1053	939
M calves	253	455	332	298
yrl bulls	122	253	248	126
2+ bulls	85	207	203	87
Total	1799	2709	2413	1977
Composition				
bull:100 cow	19	34	35	18
calf:100 cow	47	68	51	51
yrl cow:100 2+ cow	24	23	23	27
yrl bull:100 2+ bull	144	122	122	145

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.73	0.86	0.63
yrl cows	0.97	0.92	0.89
2+ cows	0.97	0.93	0.90
M calves	0.73	0.86	0.63
yrl bulls	0.98	0.95	0.93
2+ bulls	0.98	0.95	0.93
Fecundity rates			
yrl cows	0.25		
2+ cows	0.98		

Harvest		Harvest rate
F calves	34	34/332 = 0.102
yrl cows	16	16/245 = 0.065
2+ cows	114	114/1053= 0.108
M calves	34	34/332 = 0.102
yrl bulls	122	122/248 = 0.492
2+ bulls	116	116/203 = 0.571
Total	436	

[a]Spring pre-calving is late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Table 7. Gallatin elk herd population characteristics: 2400 elk in late winter modeled for stability. Harvest of 436 is stable and constant from observed '83-86 average.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	294	608	395	361
yrl cows	251	294	285	269
2+ cows	1245	1496	1451	1337
M calves	294	608	395	361
yrl bulls	147	294	282	160
2+ bulls	177	324	311	195
Total	2408	3624	3119	2683
Composition				
bull:100 cow	22	35	34	22
calf:100 cow	39	68	46	45
yrl cow:100 2+ cow	20	20	20	20
yrl bull:100 2+ bull	83	91	91	82

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.65	0.83	0.54
yrl cows	0.97	0.93	0.90
2+ cows	0.97	0.93	0.90
M calves	0.65	0.83	0.54
yrl bulls	0.96	0.88	0.85
2+ bulls	0.96	0.88	0.85
Fecundity rates			
yrl cows	0.23		
2+ cows	0.93		

Harvest		Harvest rate
F calves	34	34/395 = 0.086
yrl cows	16	16/285 = 0.056
2+ cows	114	114/1451= 0.079
M calves	34	34/395 = 0.086
yrl bulls	122	122/282 = 0.433
2+ bulls	116	116/311 = 0.373
Total	436	

[a]Spring pre-calving is late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Table 8. Wolf kill rate summary, updated from Keith (1983).

Location	Ungulate prey	Mean Kill Rate in Winter days/kill /pack	/wolf	Data Source
Isle Royale	moose	3.1	47	(1)
Isle Royale	moose	3.3	36	(2)
NE Alberta	moose	4.7	45	(3)
Alaska (Tanana)	moose	3.4	53	(4)
Alaska (Nelchina) summer	moose, caribou	7.3-15.7	22.5-117.5	(5)
Alaska (Nelchina) winter	moose, caribou	4.9-10.8	44.1-62.3	(5)
Alaska (Kenai)	moose, caribou	3.1-21.4	58.2-42.4	(6)
Alaska	caribou	1.9-4.6	13.4-32.3	(4)
Yukon	sheep, moose, caribou	7.7-9.0	31-54	(13)
SW Quebec	moose	19-90	91-250	(7)
SE Alaska	Bt deer		24.3	(4)
Ontario	Wt deer	2.2	18	(8)
Manitoba (Riding Mountain N. P.)	elk, Wt deer	3.6-6.9	14-21	(9)
W Minnesota	Wt deer	7.0	32	(10)
NE Minnesota	Wt deer	7.8	25	(11)
Alberta	elk, mule deer, moose, sheep	2.5	25	(12)

(1) Mech (1966)
(2) Peterson (1977)
(3) Fuller and Keith (1980)
(4) Holleman & Stephenson (1981)
(5) Ballard et al. (1987)
(6) Peterson et al. (1984)
(7) Messier and Crete (1985)
(8) Kolenosky (1972)
(9) Carbyn (1983)
(10) Fritts and Mech (1981)
(11) Mech (1977)
(12) Gunson (1986)
(13) Sumanik (1987) estimates provided for dall sheep only

Not enough information was available to predict the distribution of different prey items in the wolf diet in the Gallatin, because the distribution of wolves cannot be predicted and the population sizes of potentially significant alternative prey to elk, namely mule deer, moose, and beaver, are unknown. For this reason, we estimated the effect of wolf predation upon the elk population using the assumption that elk will constitute between 75% and 90% of the prey. Two predation rates that encompassed the potential range of kill rates were used for the Leslie matrix models: low predation at 75% of 12 ungulates killed/wolf/year = 9 elk killed/wolf/year, and a high of 90% of 28 = 25 elk killed/wolf/year (Table 9).

Carbyn (1975, 1983) considered bull elk more vulnerable to predation than cows. In Riding Mountain National Park, Carbyn (1983) reported that calves comprised 34% of the wolf-killed elk, and animals over seven years of age comprised 40%. Elk calves were killed most frequently in early midwinter but adult cows were more frequently taken in late winter (Carbyn 1983). All animals examined had high femur marrow fat levels and lacked skeletal or hoof abnormalities. Carbyn (1983) reported that 39 of 57 adult elk killed by wolves were cows, a sex ratio of 46 bulls:100 cows. No sex ratios in the harvest or the population were given, but that ratio appears high and suggests that more bulls were being taken than expected based on their occurrence in the population. Cows are often found in large groups that may facilitate detection of predators and minimize probability of predation. Bulls occur in smaller groups, are often injured in fights, and enter the winter in poor condition, making them more vulnerable to predation than cows. Carbyn (1983) believed that cows were either more alert than bulls or had evolved better escape mechanisms than bulls.

The relative proportions of calves, adults and older elk taken in Jasper and Riding Mountain National Parks by wolves was quite similar. Averages were 37.5% calves, 29% adults and 33.5% older animals. In Riding Mountain National Park, calves were taken 1.79 times greater than their estimated occurrence in the population, while adults were taken 0.63 times as much, and old animals were taken in proportion to their occurrence. Carbyn (1983) concluded that more elk calves and fewer adult elk (1-11.5 years old) were killed by wolves than by hunters. For the Leslie matrix models we used a ratio of 0.46 bulls aged 1 or older to 1 cow killed, and the averages of 37.5% calves, 29% adults, and 33.5% old animals in the wolf kill (Table 9). We assumed that equal proportion of male and female calves were killed (Table 9).

Three kill rates were used for the balance models. Reported biomass consumption by wolves ranged from 2.0 kg/wolf/day (Fuller 1989) to 7.2 kg/wolf/day (Peterson 1977) with an average of 4.4 kg/wolf/day for 14 studies reported by Fuller (1989). Mech (1977) estimated that maintenance requirement for wolves was 1.7 kg/wolf/day, and that wolves can eat as much as three times their maintenance requirement (5.1 kg/wolf/day). We estimated the number of elk needed by sex and age to meet the 2.5 and 5.1 kg/day/wolf consumption rate and modeled these estimates as kill rates in the balance models (Table 10). Partitioning the kill was derived as follows. Summer was estimated as 150 days and winter 215 days. We assumed that 85% of the biomass needs would be met by elk. Summer consumption was 2.5 kg/wolf/day x 150 days x

Table 9. Partitioning the elk kill per wolf per year for the Gallatin and Sand Creek elk herd Leslie matrix models.

1. Number of ungulates taken/wolf/year= 12-28
   if elk are 75% of diet = 9-21
   if elk are 90% of diet = 11-25

2. Assuming adult sex ratio of 46 bulls:100 cows, age ratios of 37.5 calves:29.0 adults:33.5 old in the wolf take, then of those 9-25 elk taken/wolf/year,

   3.6-9.4 elk will be calves, sex ratio equal;
   3.0-7.2 elk will be aged 1-7, with
   0.6-2.3 males, 2.4-4.9 females;
   3.0-8.4 elk will be aged 8 or older, with
   1.0-2.0 males, 2.0-6.4 females.

3. Gallatin: proportion of each sex/age group of fall elk population of 2314 taken/wolf/year will be:

	MALES		FEMALES	
	IN POPN.	PROPORTION TAKEN/ WOLF/YEAR	IN POPN.	PROPORTION TAKEN/ WOLF/YEAR
CALVES	468	.004-.010	468	.004-.010
ADULTS	300	.002-.008	948	.002-.005
OLD	1	1-	129	.015-.049
TOTAL	769		1545	

4. Sand Creek: proportion of each sex/age group of fall elk population of 5372 taken/wolf/year will be:

	MALES		FEMALES	
	IN POPN.	PROPORTION TAKEN/ WOLF/YEAR	IN POPN.	PROPORTION TAKEN/ WOLF/YEAR
CALVES	856	.0035-.004	849	.0035-.004
YEARLINGS	743	.0005-.001	737	.0003-.0004
ADULTS	665	.0009-.001	1522	.0005-.0007
TOTAL	2264		3108	

0.85 proportion is elk = 319 kg of elk/wolf, or 2.1 kg of elk/wolf/day. Winter consumption was estimated at 2.5 kg/wolf/day x 215 days x 0.85 = 457 kg of elk/wolf(2.1 kg of elk/wolf/day). At 5.1 kg/wolf/day consumption, elk during summer comprised 650 kg/wolf and in winter was 932 kg/wolf (4.3 kg elk/wolf/day). At the 2.5 kg/wolf/day consumption rate, annual kill was 6.6 elk/wolf/year (Table 10), or 45% of the lowest reported kill rate in an ungulate system containing elk (Gunson 1986, Table 8). Of 145 ungulates killed by wolves, Gunson (1986) reported that 79 (54%) were elk,. At 5.1 kg/day/wolf the kill rate was 13.4 elk/wolf (Table 10), 92% of the lowest reported kill rate in an ungulate system containing elk (Gunson 1986) and 51% of the highest reported kill rate on elk (Carbyn 1983, Table 8). The third estimate used the upper value of 26 ungulates killed/year (Carbyn 1983, Table 8); 80% of these killed were elk, resulting in an annual kill of 21 elk (Table 10). At this kill rate, summer biomass consumption was estimated at 4.9 kg elk/wolf/day, and during winter was 7.7 kg/day/wolf for an annual average intake of 6.6 kg elk/day/wolf. Because the reported kill rates in systems containing elk ranged from 14.6 to 26.1 ungulates/wolf/year (Table 8), the first estimate of 6.6 elk killed/wolf/year provided a low kill rate (LOW), the second of 13.4 elk killed/wolf/year a moderate kill rate (MODERATE), and the third of 21 elk killed/wolf/year a high (HIGH) kill rate.

Projections of the Effects of Predation on the Gallatin Elk Herd

Leslie Matrix Projections

The Leslie matrix models included scenarios at high and low predation rates with 10 wolves, after preliminary investigations with more wolves suggested that no adjustments in either compensation in survival or reductions in hunter harvest were realistic. Predation rates were high when elk constituted 90% of the wolf diet (90% of 28 ungulates killed) and low when elk constituted 75% of the wolf diet (75% of 12 ungulates killed). Three harvest strategies were explored: elk harvest at current estimated levels, antlerless elk harvest at half the current level, and harvesting of bull elk only. Compensatory responses in survival were modeled as 5% increases in survival of all sex and age classes.

When no compensatory responses in survival are used and harvest was not changed, the elk population declined at either high or low predation rates by 10 wolves (Table 11). When the antlerless harvest is reduced to half the current level, (5% of cows and calves available prior to the hunt) the elk population increased at low predation rates but declined at high predation rates. The population increased at either level of predation if only bulls were taken. When survival of all sex/age classes is increased 5%, the model population responded by increasing at low predation rates but declined at the higher rates.

Table 10. Distribution of assumed predation, and approximate biomass consumption by wolves on elk, by age and sex, used in the Gallatin elk herd balance models. Utilization is proportion of carcass mass consumed. LOW, MODERATE, and HIGH kill rates are presented.

Sex-age	Number of elk killed/wolf LOW	MODERATE	HIGH	Utilization	Mass of prey (kg)	Consumption (kg/wolf) LOW	MODERATE	HIGH
Summer (150 days)								
Female								
calves	1.1	2.2	3.5	0.80	30	26	53	84
yearling	0.13	0.27	0.3	0.75	240	23	49	54
2+ cows	0.57	1.23	1.2	0.75	240	103	221	216
Male								
calves	1.1	2.2	3.5	0.80	30	26	53	84
yearling	0.35	0.75	0.75	0.75	260	63	146	146
2+ bulls	0.35	0.75	0.75	0.75	260	63	146	146
Sub-total	3.6	7.40	10.0			304	668	730
Winter (215 days)								
Female								
calves	0.5	0.95	2.0	0.75	114	46	87	171
yearling	0.16	0.36	0.6	0.75	240	29	65	108
2+ cows	0.74	1.64	2.4	0.75	240	133	295	432
Male								
calves	0.5	0.95	2.0	0.75	114	46	87	171
yearling	0.55	1.1	2.0	0.75	260	107	215	390
2+ bulls	0.55	1.1	2.0	0.75	260	107	215	390
Sub-total	3.0	6.1	11.0			468	964	1662
Total	6.6	13.4	21.0			772	1632	2392

Table 11. Rates of increase of the model Gallatin elk population with different levels of wolf predation, harvest strategies, and survival rates. Wolf predation is specified to be exerted by 10 wolves. Low level of wolf predation specify 9 elk killed; high level 25 elk killed.

Hunter harvest	Level of wolf predation	Survival	Finite rate of increase of elk population
1983-86 level[a]	none	([b])	1.0001
1983-86 level	low	no change	0.9683
1983-86 level	high	no change	0.9086
50% of bulls	low	no change	1.0689
50% of bulls	high	no change	1.0055
Cows & calves 5%	low	no change	1.0193
Cows & calves 5%	high	no change	0.9389
1983-86 level	low	up 5%	0.9936
1983-86 level	high	up 5%	0.9405
50% of bulls	low	up 5%	1.1080
50% of bulls	high	up 5%	1.0378
Cows & calves 5%	low	up 5%	1.0493
Cows & calves 5%	high	up 5%	0.9897

[a]Antlerless harvest = 10.5%, bull harvest = 50%.
[b]Survival rates for calves= 0.55, bulls =0.90, and cows = 0.95.

Balance Models

Two methods of simulating predation were used with the balance models. One method used constant and fixed survival, fecundity, harvest, and predation rates for the population with a range of wolf numbers. Over time this is unrealistic because populations, harvest, and predation are not stable. The second models used varying harvest rates, which managers can control. These models explored a variety of harvest strategies by examining calf harvest ranging from 1% to 12%, cow harvest from 1% to 12%, and bull harvest from 35% to 60% of the prehunt population (3,744 different scenarios). Ranges of harvest management options for populations with wolf predation were demonstrated. For each of these methods, LOW, MODERATE, and HIGH wolf kill rates were simulated. The population at 2,400 (Table 7) was simulated because it represented the most realistic population estimate. With the variable harvest models, more than 11,000 different scenarios were run for each individual wolf, or 336,960 runs for a range of 1 to 30 wolves for each population evaluated. Compensatory responses were not modeled because the Gallatin herd was heavily hunted, and was probably near maximum productivity.

Graphs of population size and harvest during an initial five year period from the models assuming constant survival, birth, and harvest rates (Table 7), and two levels of predation (LOW and MODERATE, Table 10) are shown in Figs. 3a-3d for a winter population of 2400. Since these models were derived from average harvest and assumed stable populations, any additional mortality caused a population decline (Figs. 3a and 3b) and harvest decline (Figs. 3c and 3d) in the absence of management changes. With more wolves, the decline in population size and harvest was more rapid. These results show the potential short-term impacts of constant wolf predation in the absence of management changes or wolf response.

These models assumed no change in harvest rates, something managers can control. Reductions in population size can be countered by temporarily restricting harvest to allow population increases, resulting in population fluctuations around a stable mean, and/or by managing wolves. Wolf numbers might also decline naturally. If prey populations decline considerably it is unlikely that wolves would remain in an area unless an adequate alternate prey base was available. If alternative prey supported a large wolf population after a principle prey decline, then the principle prey population could be held at a low "equilibrium". If wolves died or moved out of an area, prey populations would rebound if harvest and weather were favorable. Winterkill might be additive to wolf predation and result in steeper declines than shown in Fig. 3. Mild winters, better forage conditions, and alternative prey would buffer the effects of wolf predation.

The models that used variable harvest rates while maintaining fixed survival and fecundity rates for a winter population size of 2,400 (Table 7) indicated that a narrow range of harvest could be obtained for a given number of wolves (Fig. 4). Results of these models were for stable elk populations with constant wolf predation for 15 years. The LOW (Fig. 4a), MODERATE (Fig. 4b), and HIGH (Fig 4c) kill rates are presented. The range of harvest was due to

different harvest rate combinations for different sex/age classes. Varying harvest rate as a management option provided more harvest opportunities than the fixed harvest rate model (Fig. 3). With increasing wolf predation, the population could be held stable only by decreasing harvest levels. This was achieved in the model by reducing cow harvest. Bulls then made up a larger percent of the total harvest (Fig. 5). Bulls averaged 55% of the total harvest between 1983 and 1985. No opportunity to increase total harvest or offset harvest reductions from reducing cow harvest was possible because bulls were already being harvested near maximum rates.

The presence of wolves forced a reduction in cow elk harvest to maintain a stable elk population. The reduction in antlerless (calf and cow) harvest needed to maintain a stable population in the presence of wolf predation at LOW and MODERATE kill rates are shown in Fig. 6. For a set number of wolves, antlerless harvest rates below the MODERATE predation equilibrium line would allow elk to increase. Harvest rates above the LOW predation equilibrium line would cause a population decline. The area between the two lines is the range of predation (assuming elk were 85% of the wolf diet) that may occur, and the elk population will either increase or decrease depending on intensity of predation, alternative prey, and antlerless elk harvest rate, all other things being constant (survival and fecundity). If cow elk were killed in proportion to their occurrence in the population, rather than the estimated proportions used (Table 10), then cow harvest reductions greater than those projected in these models would be required and total harvest would be less than projected.

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The variable harvest model with a precalving population of 2,400 elk indicated that average annual average harvest could be between 350 and 460 elk, depending on wolf kill rate, support five adult wolves (Fig. 4), with no change in elk survival rates, and remain stable. With five wolves, cow and calf harvest rate would be reduced to between 6% and 7% (Fig. 6), and the bull harvest rate would be near 50% of the prehunt bull population.

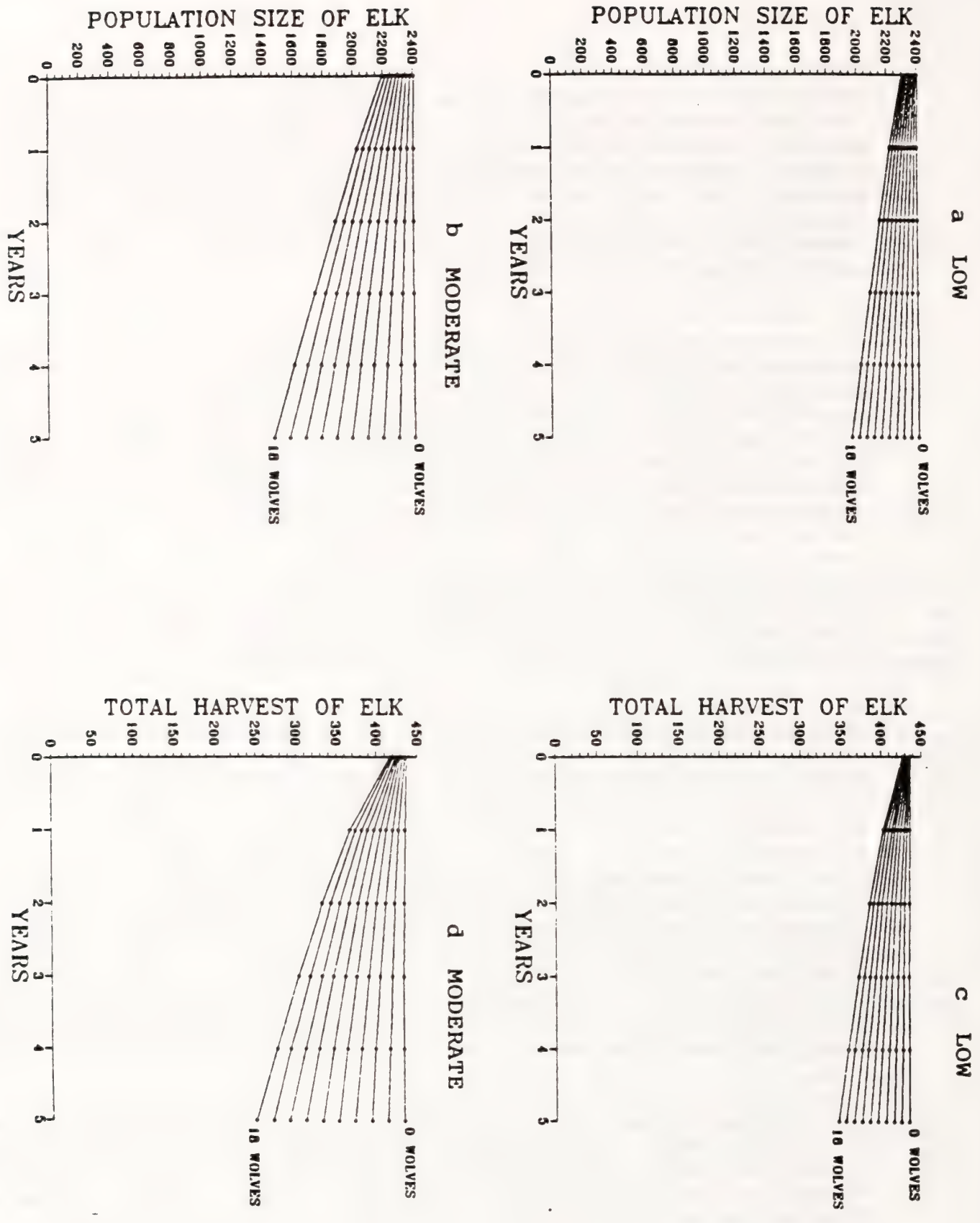

Fig. 3. Potential initial 5-year wolf restoration impacts on the Gallatin elk population size (a,b) and total hunter harvest of elk (c,d). Model elk popultaion initially at 2400 in spring, pre-calving. Models assume no changes in elk management, or wolf numbers, distribution, or behavior. LOW (a,c) and MODERATE (b,d) wolf kill rates are presented.

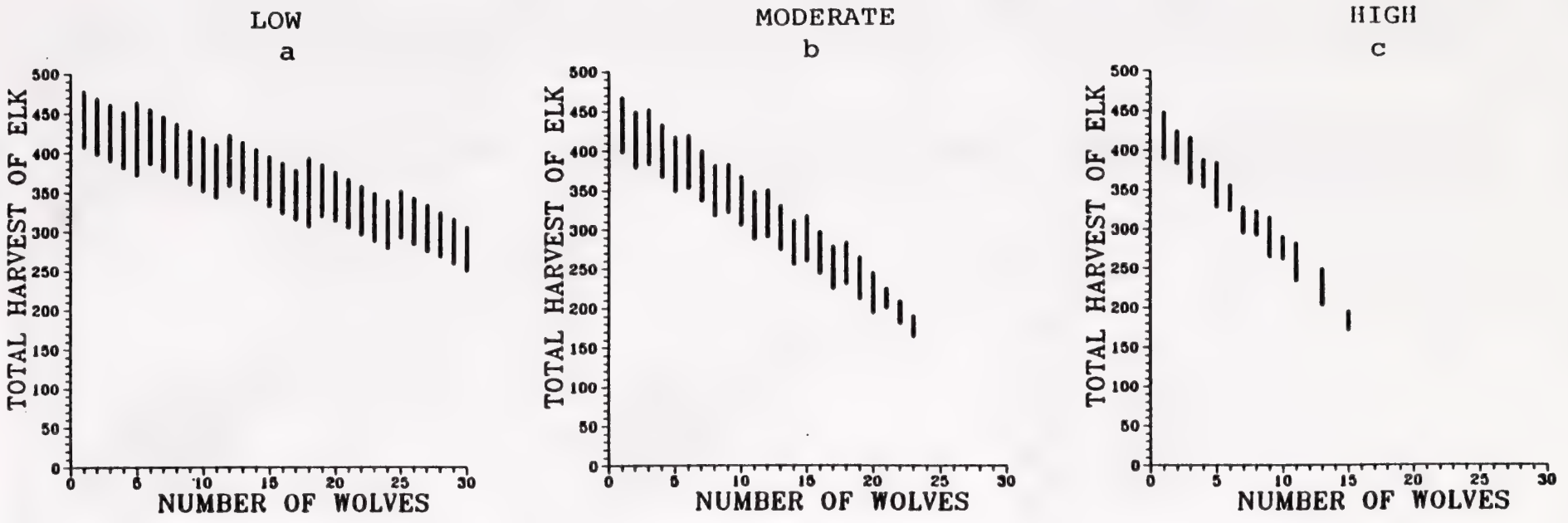

Fig. 4. Range in potential total hunter harvest of elk related to number of wolves for the LOW (a) MODERATE (b), and HIGH (c) kill rates evaluated in the Gallatin elk herd model with a spring pre-calving population of 2400 elk. Range in total harvest results from examing many sex/age combintations of hunter harvest rartes.

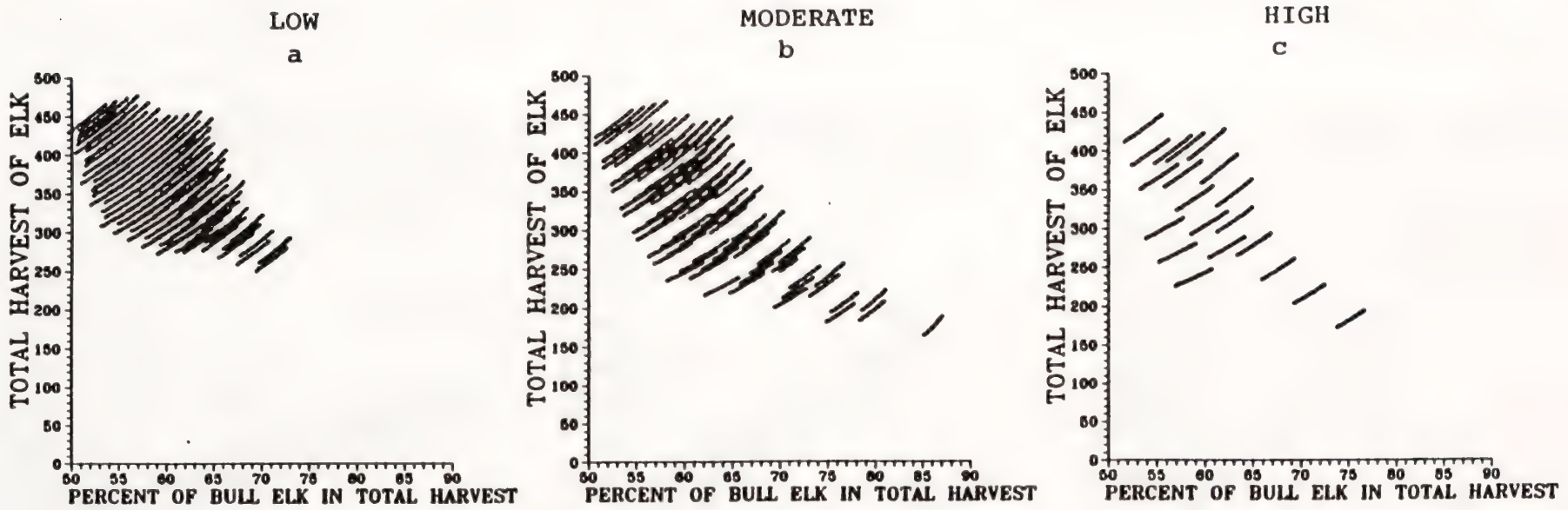

Fig. 5. Range inpotential total hunter harvest of elk related to percent of bulls in total harvest for the LOW (a), MODERATE (b), and HIGH (c) kill rate scenarios evaluated in the Gallatin elk herd model with a spring pre-calving popula;tion of 2400. Ranges in total harvest relate to the range of wolves shown in FIg. 4.

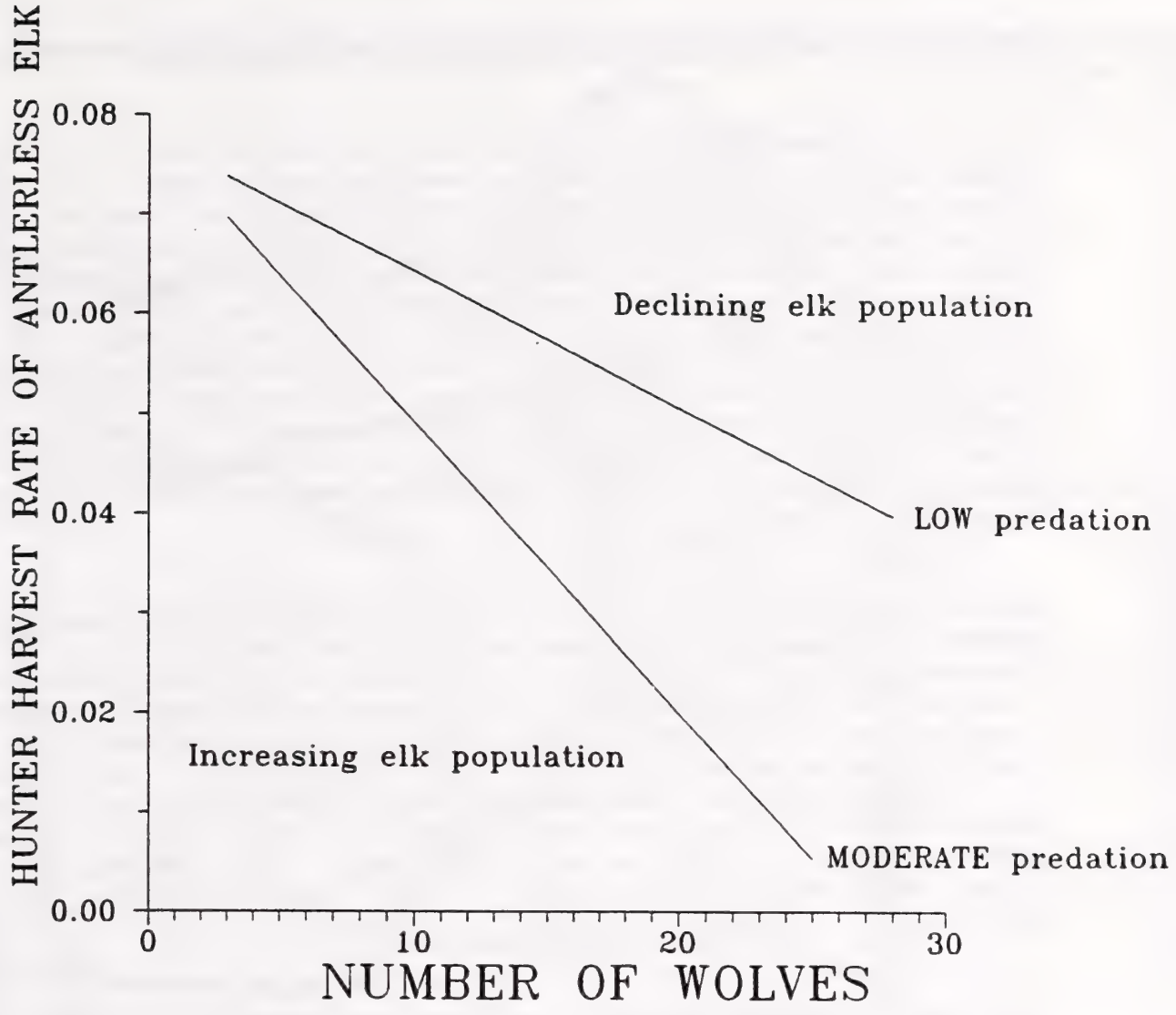

Fig. 6. Change in hunter harvest rate of antlerless elk needed to maintain a stable population at varying number of wolves for the LOW and MODERATE kill rates evaluated in the Gallatin elk herd model with a spring pre-calving population size of 2400 elk. Harvest rates below lines result in increasing populations; harvest rates above result in declining populations, with no change in survival or fecundity. Region of uncertainty exists between lines: harvest rate will be dependent upon wolf response and predation rate on elk.

Sand Creek Elk Population Characteristics: Balance Models

Winter range for the Sand Creek elk herd is located west of U.S. Highway 20, mostly north of State Highway 33 between Rexburg and Sage Junction, east of Interstate 15, and south of a line drawn between Dubois and Island Park, Idaho, in hunt units 60, 60A, and 63A (Brown 1985, Fig. 7). In summer, animals are distributed throughout units 60, 60A, 61, 62, 62A, 63A, southwestern Yellowstone National Park, Harriman State Park (Fig. 7), Montana, and probably in Wyoming hunt area 73 ("Targhee Herd"). The eastern edges of unit 61, unit 62A, and the northeastern corner of unit 62 border Yellowstone National Park. The distribution of elk on summer ranges was documented by Brown (1985, Fig. 7, Table 12). There has been documented interchange of elk among the Jackson (Wyo.) and Wall Creek Game Range (Mont.) herds (J. Naderman, Idaho Dept. Fish & Game, pers. comm.). Fall migration routes were documented by Brown (1985, Fig. 8).

Winter population trend counts for the Sand Creek elk herd increased between 1959 and 1983, with oscillations since 1983 around 2,500 (Fig. 9, Table 13). There was no significant linear relationship between population trend count and year between 1981 and 1989 ($P = 0.27$) indicating no significant trend in population size with time. Naderman (pers. comm.) estimated that the trend counts comprised about 80% of the entire Sand Creek herd, giving an average of 3,125 elk in the herd during winter. Brown (1985) estimated the summer prehunt population of the Sand Creek herd to be 4,900 animals in 1983, after the 1982-1983 winter trend count of 2,959 animals. The five-year elk management plan (Toweill et al. 1985) specified that a summer population of 4,750 elk be maintained to produce a harvest of 935 animals.

Herd composition counts on the northern range were done from the ground, usually in December. Average bull:cow:calf composition between 1980 and 1987 was 22:100:54 (Table 13). Yearling bull:2.5+-year-old bull ratios averaged 86:100 excluding the 1984-1985 classification of 181:100. Specific age structure data for the population was obtained during the 1980-1982 hunting seasons (Table 14), but none since. The present age structure is probably younger than it was in 1980-1982 (J. Naderman pers. comm.). Additional age structure data included herd composition counts (Table 13) and the age structure of harvested bulls (Table 15). We initially assumed that the Sand Creek herd in late winter (spring precalving) was composed of 22 bulls:100 cows:54 calves, with 20% of the females being yearlings and 46% of the bulls being yearlings (Table 13).

Excluding the high elk harvest in 1988, harvest between 1980 and 1987 averaged 958 animals (Table 16). Fluctuations were due to weather, population size, and harvest regulation changes. There were no significant relationships between general, controlled, or total harvest and year, indicating no trend with time. Fall harvest between 1979 and 1988, however, was linearly related to the trend count the previous winter (Fig. 10, excluding 1983; general harvest = 0.243 x

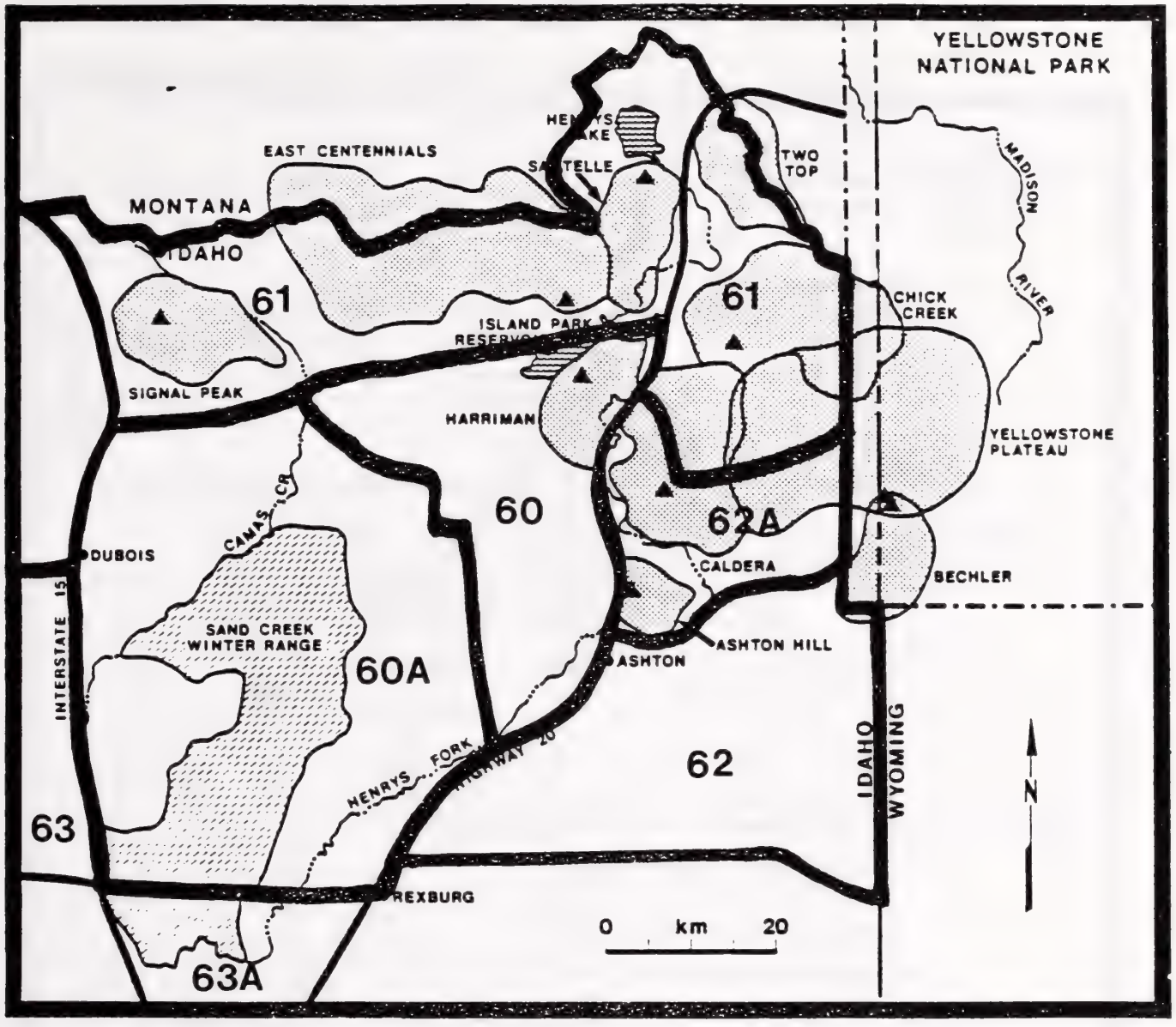

Fig. 7. Summer distribution of elk that winter on the Sand Creek winter range. Summer subpopulation ranges are represented by shaded areas. Unit boundaries represented by bold lines. Adapted from Brown (1985).

Table 12. Distribution of Sand Creek elk herd in summer and harvest rate of radio-collared cow elk (from Brown 1985).

Unit	Subpopulation	Number radio-collared	Percent radio-collared	Percent of elk observed	Number of days on summer range	Harvest rate of radio-collared cows	Notes
61	Signal Peak	3	5.8	4.8	170-191	0	
61	East Centennials	6	11.5	18.8	108-206	44.4%	
61	Sawtell	2	3.9	2.7	113-159	0	
61	Two Top	1	1.9	3.1	124	0	
61,YNP	Chick Creek	6	11.5	3.4	128-154	13.3%	2 killed while migrating
61,62A	Caldera	5	9.6	7.2	111-152	37.5%	2 killed in 60 while migrating, 1 on summer range in 61
61,62A,YNP	Yellowstone Plateau	4	7.7	6.8	136-185	11.0%	1 killed while migrating
62,62A,YNP	Bechler	6	11.5	17.1	104-162	22.0%	1 killed while migrating
62A	Ashton Hill	2	3.9	1.7	153-168	0	
60	Harriman	15	28.8	32.8	125-210	15.0%	2 of 13 killed while migrating after harvest restructure

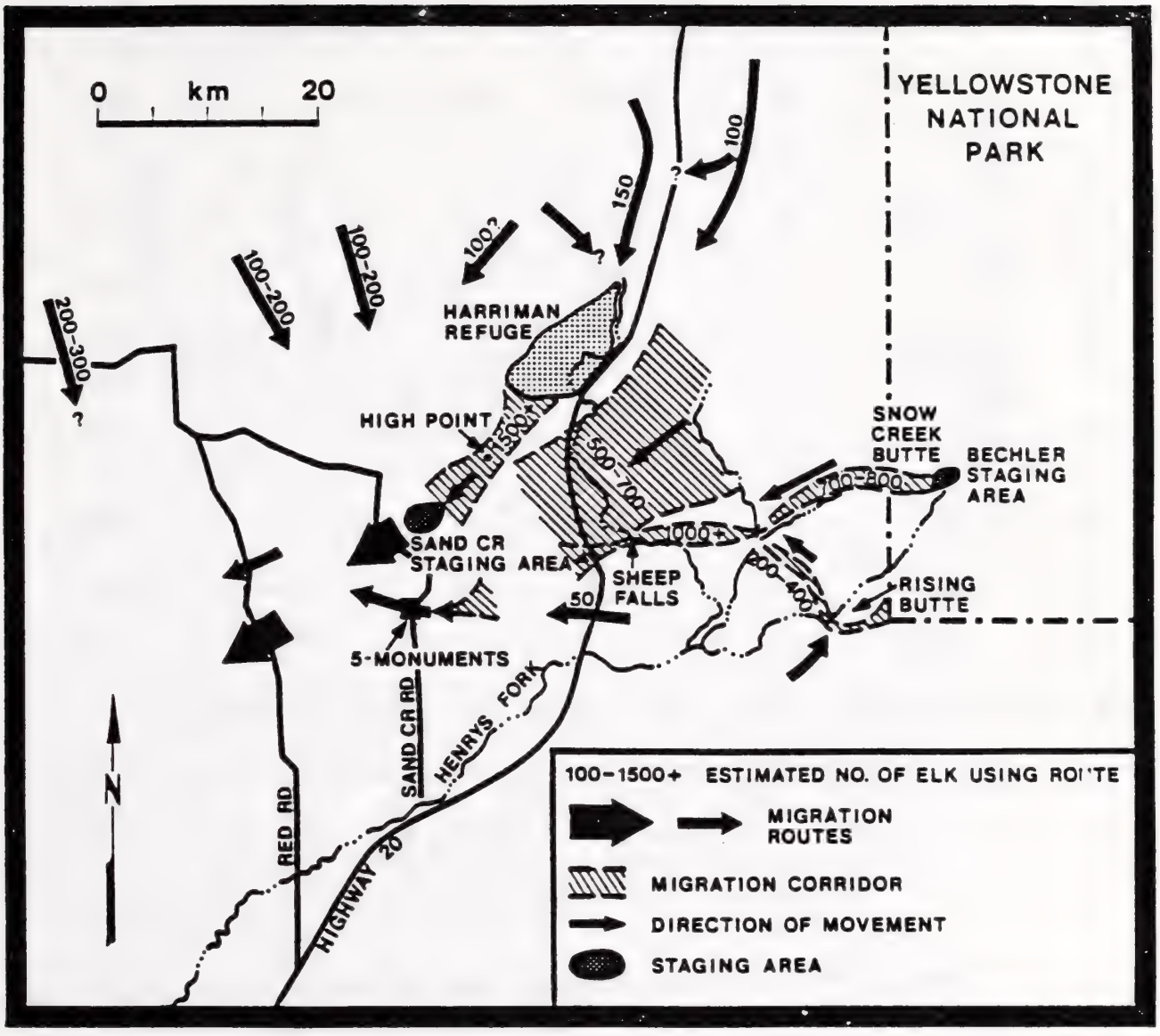

Fig. 8. Fall migration routes and staging areas of the Sand Creek elk herd, 1981-1983 (from Brown 1985).

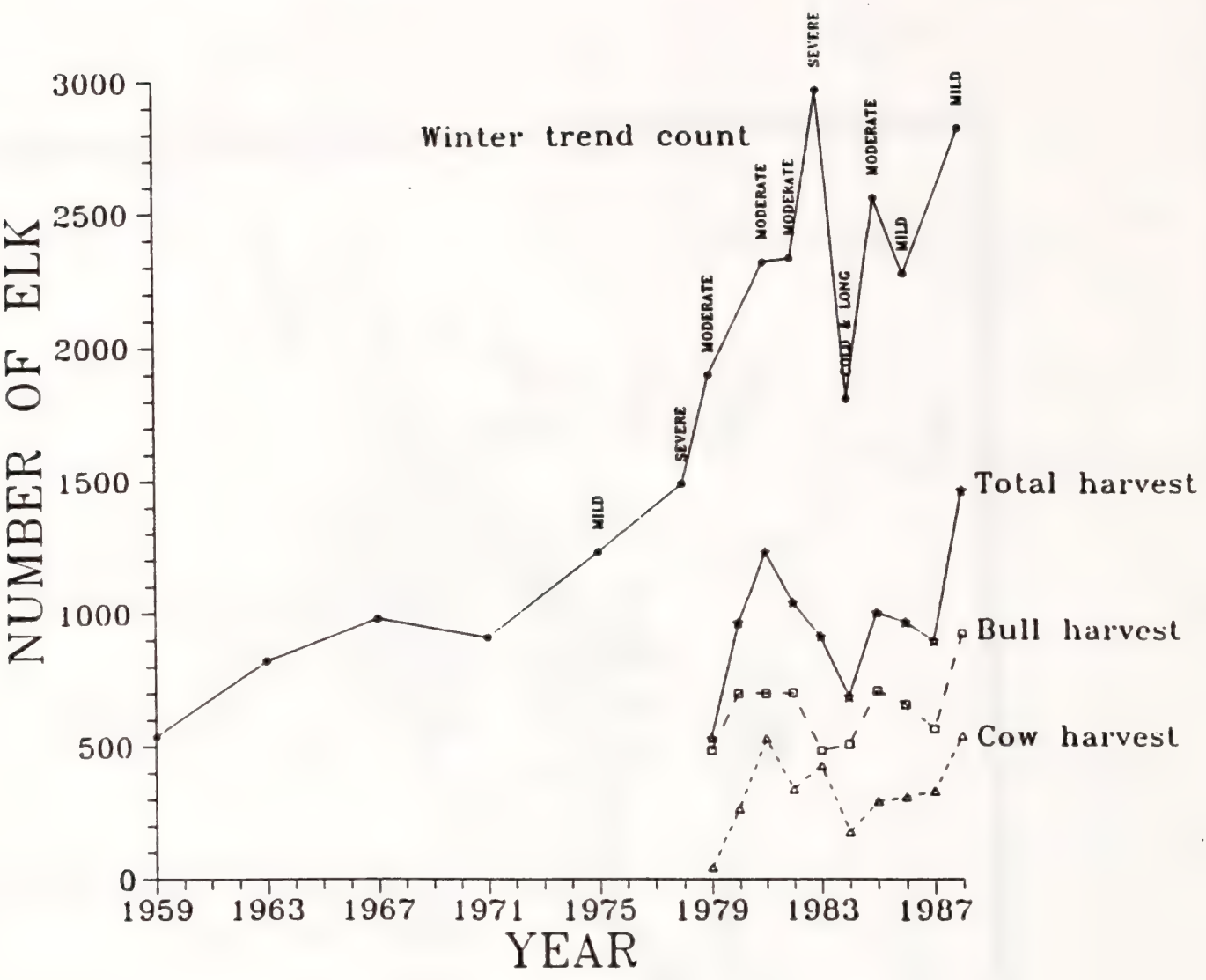

Fig. 9. Winter trend count of elk, winter severity, and harvest by year for the Sand Creek elk herd.

Table 13. Population characteristics of the Sand Creek elk herd in winter.

Year	Winter trend count[a]	Bulls			Antlerless	Calf:Cow[b]	Bull:Cow[c]	Yearling: Branch-antlered bull ratio
		Yearling	Branch-antlered	Total				
88-89	(2441 minimum estimate)			-	-	-	-	-
87-88	2815	117	231	348	2469	54	33	67[d], 51[e]
86-87	-	-	-	-	-	46	20	108[d]
85-86	2269	84	119	203	2066	60	19	100[d], 71[e]
84-85	2553	-	-	291	2262	44	18	181[d]
83-84	1803 (April)		-	-	-	53[f]	20	82
	2287 (January)		-	241[g]	2046[g]	57[g]	19[g]	-
82-83	2959	148	157	305	2654	65	18	96[d], 95[e]
	-	-	-	-	-	56[g]	18[g]	-
81-82	2327	136	201	337	1990	50[h]	25[i]	68
80-81	2310	135	169	304	2006	50[h]	23[i]	80
Avg.	2502	-	-	-	-	54	22	86

[a]Number of elk counted on Sand Creek winter range (Units 60 and 60A) from aerial census for annual trend count. Usually done in January.
[b]Number of calves:100 cows from ground herd composition counts usually done in December.
[c]Number of bulls:100 cows from ground herd composition count.
[d]Yearling bulls:100 adult bulls from herd composition count.
[e]Yearling bulls:100 adult bulls calculated from trend count.
[f]Calculated from approximate distribution of elk on winter range.
[g]Data presented in Brown 1985.
[h]Assumed ratio (Oldenburg et al. 1983a:274).
[i]Calculated from assumed calf:cow ratios.

Table 14. Age structure of Sand Cr. male (M) and female (F) elk harvested 1980-1982 from Units 60, 61, 62, and 62A (from Oldenburg et al. 1983a).

	PERCENT IN EACH AGE CLASS									
Age	1980-82 Unit 60		1980-82 Unit 61		1981-82 Unit 62		1981-82 Unit 62A		1980-82 Combined	
	M	F	M	F	M	F	M	F	M[a]	F[b]
1.5	63	23	39	21	35	25	41	22	49	22
2.5	24	19	32	26	27	25	32	18	28	21
3.5	7	16	14	13	16	25	7	15	10	16
4.5	3	10	8	8	1	--	8	18	5	9
5.5	1	9	3	12	5	10	5	4	3	10
6.5	1	4	2	2	5	10	1	--	1	3
7.5	1	4	2	3	5	--	1	--	1	3
8.5	--	5	--	7	2	--	1	7	1	5
9.5	1	1	--	3	1	--	3	4	1	2
10.5	1	3	1	1	--	5	--	--	1	2
11.5	--	2	--	1	1	--	--	--	1	2
12.5	--	2	--	1	--	--	--	4	--	2
13.5	--	1	--	1	--	--	--	--	--	1
14.5	--	1	--	--	--	--	--	--	--	1
15.5	--	--	--	--	--	--	--	--	--	1
16.5	--	--	--	--	--	--	--	--	--	--
17.5	--	1	--	--	--	--	--	--	--	1
Sample Size	350	210	252	126	87	20	147	27	836	383

[a]Survival rate of males 2.5 and older: 0.523.
[b]Survival rate of females 2.5 and older: 0.733.

Table 15. Yearling bull elk harvest as a percent of total bull harvest for general hunts on the Sand Creek elk herd.

	Percent of bull harvest that is yearling				
	Hunt Unit				
Year	60	61	62	62A	Total
1988	68	39	33	37	51
1987	64	38	15	41	47
1986	70	42	28	38	59
1985	54	18	22	50	43
1984	60	29	10	33	45
1983	69	45	63	67	61
1982	76	36	32	41	52
1981	50	42	33	39	44
1980	65	39	63	48	51
Average	64	36	33	44	50

Table 16. Sand Cr. elk herd harvest characteristics by unit, hunt (GH=general hunt, CH=controlled hunt), and sex (M=Males, F=antlerless and may include calves) derived from telephone survey (summarized from Oldenburg et al. 1980a, 1981a, 1982a, 1983a, 1984a, 1985a, 1986a, 1987a, and 1988a, and Kuck et al. 1989a).

	Hunt Unit																			
	60				61				62				62A				Total			Other documented mortality
	GH	CH			GH	CH			GH	CH			GH	CH			(incl. 63A)			(incl. archery &
Year	M	M	F	T	M	M	F	T	M	M	F	T	M	M	F	T	M	F	T	muzzleloader hunts)
1988	253	43	288	584	309	0	0	309	80	102	54	236	45	58	181	282	921	537	1458	--
1987	191	0	137	328	250	0	0	250	42	27	43	112	25	27	150	202	563	331	894	28
1986	262	3	180	445	211	0	0	211	62	40	34	136	32	46	94	172	656	308	964	39
1985	246	24	159	429	239	7	13	259	68	20	10	98	67	32	109	208	707	292	999	56
1984	193	0	38	231	134	0	39	173	77	48	39	164	26	29	62	117	507	178	685	61
1983	174	22	190	386	156	17	86	259	39	24	68	131	0	39	78	117	483	427	910	112
1982	192	17	90	299	259	6	117	382	67	59	65	191	67	31	66	164	699	338	1037	--
1981	283	44	256	583	157	14	178	349	31	48	37	116	63	58	57	178	698	528	1226	--
1980	284	18	154	456	185	8	37	230	62	8	16	86	82	51	57	190	698	264	962	--
Avg.	231	19	166	416	211	6	52	269	59	42	41	141	45	41	95	181	659	356	1015	59

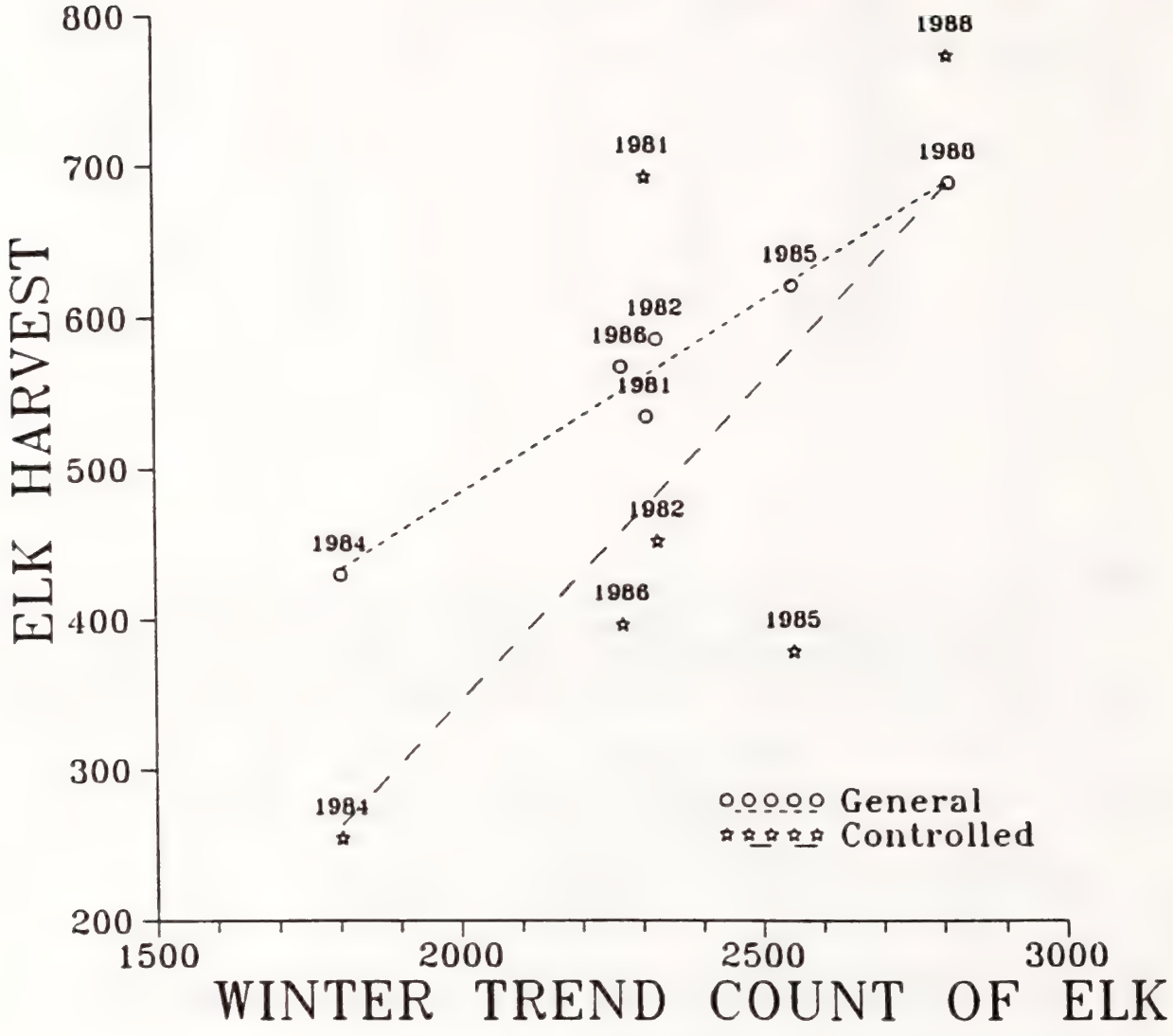

Fig. 10. Relationship between general and controlled hunt harvest and previous-winter trend count of elk, excluding 1983 data, for the Sand Creek elk herd.

trend count; r^2 = 0.99; P < 0.01; controlled harvest = 0.419 x trend count - 493; r^2 = 0.50; P = 0.11; and total harvest = 0.439 x trend count; r^2 = 0.97; P < 0.01).

The strong relationship between general harvest and trend count was the hunter functional response to elk numbers. The poor relationship between the controlled hunt harvest and trend count probably reflected variation due to weather effects on migrations, number of permits (Table 17), changes in regulations (Table 18), or percent of hunters with controlled hunt permits actually participating in the controlled hunt.

The harvest rate of radiocollared cows ranged from 0% to 44% among different summer subpopulations (Table 12). Many of the cows were migrating when harvested. Roughly 80% of radiocollared bulls outside of Yellowstone National Park and Harriman State Park were harvested between 1985 and 1987 (Oldenburg et al. 1988a). Bulls that summered in Yellowstone were also harvested while migrating to winter range. Because there was no trend in harvest with time, the average harvest of 958 elk between 1980 and 1987 was used in our models, and 50% of the bull harvest was assumed to be yearlings (Table 15); 25% of the cow harvest was assumed to be yearlings (Table 14); and 6% of the antlerless harvest was assumed to be calves of equal sex ratio.

Several changes in hunt units have occurred since 1980 that might have affected harvests: 1) in 1981, the elk and deer seasons were split to reduce bull elk harvest; 2) unit 60A was formed in 1984 from unit 60 and was closed to elk hunting, but was opened for controlled hunts in 1988; 3) hunts have occurred in unit 63A despite Management Plan objectives of zero harvest; and 4) controlled hunts in units 261 and 262 were split into two hunts in 1982 (Table 17). Additional changes in number of controlled hunt permits and season length have occurred (Tables 17, 18).

Resident animals were usually harvested during general seasons unless snow forced elk to migrate early. Special permit hunts (controlled hunts) were designed to control elk populations, prevent depredations, and reduce the impact elk have on winter range. The controlled hunts, 262 and 262A, were designed to harvest elk migrating out of Yellowstone National Park and Wyoming. The unit 60 controlled hunts were redesigned in 1983 to harvest resident animals from Harriman State Park (closed to hunting) as they migrate to the winter range. These 260 hunts also take elk migrating from other areas (e.g., Yellowstone N.P.), but the proportions are unknown and dependent upon weather. The general harvest from unit 61 more likely reflects animals that summer along the Montana boundary in the East Centennials' subpopulation than from Yellowstone. The controlled hunt 261, which ended in 1985, may have included a few animals that summered along the Yellowstone National Park boundary.

Elk that winter in Idaho and summer in Wyoming might be harvested in Wyoming hunt area 73. Additionally, elk that summer in the Bechler Meadows area of Yellowstone might be harvested in Wyoming while migrating to Idaho. However, the Wyoming elk harvest in hunt area 73 has been low (average of 50 elk

Table 17. Number of controlled hunt permits for elk by hunt and year.

Hunt	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
260	---	---	300	---	---	---	---	---	450	450
260-1	150	225	---	225	150	300	300	300	---	---
260-2	150	225	---	225	150	150	150	150	---	---
260A	---	---	---	---	---	---	---	---	100	---
260A-1	---	---	---	---	---	---	---	---	---	60
260A-2	---	---	---	---	---	---	---	---	---	180
261	150	450	---	---	230	400	---	---	---	---
261-1	---	---	100	100	---	---	---	---	---	---
261-2	---	---	350	350	---	---	---	---	---	---
262	100	200	---	---	---	---	---	---	---	---
262-1	---	---	100	100	65	65	65	65	65	65
262-2	---	---	150	150	100	150	150	150	150	150
262A-1	100	200	200	200	130	130	130	100	100	350
262A-2	30	50	75	50	75	50	60	60	70	70
262A-3	150	300	300	300	200	200	200	200	250	70
262A-4	---	---	---	---	---	50	60	60	70	---
263A-2	---	---	---	---	---	---	---	---	15	50
Total	830	1650	1575	1730	1130	1510	1130	1100	1335	1535

Table 18. Number of days and sex of elk hunting seasons by Unit and year. M-male, A-antlerless, E-either sex.

Hunt	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Gen.	5,M	5,M	5,M	5,M	5,M	5,M	5,M	5,M	5,M	5,M
Arch.[a]	44,E	23,E	28,E	28,E	28,E	28,E	28,E	28,E	28,E	28,E
Muzzl.[b]	23,E	23,E	16E,7M	16E,7M	16E,7M	16E,7M	23,E	23,E	23,E	23,E
260	---	---	12,A	---	---	---	---	---	40,A	37,A
260-1	12,A	14A,5E	---	14,A	14,A	26,A	26,A	25,A	---	---
260-2	12,A	5,E	---	14,A	14,A	14,A	23,A	23,A	---	---
260A	---	---	---	---	---	---	---	---	65,E	---
260A-1	---	---	---	---	---	---	---	---	---	18,E
260A-2	---	---	---	---	---	---	---	---	---	42,A
261	5E,5A	14A,5E	---	---	12,A	10,A	---	---	---	---
261-1	---	---	12,A	12,A	---	---	---	---	---	---
261-2	---	---	12,A	12,A	---	---	---	---	---	---
262	16,E	23,E	---	---	---	---	---	---	---	---
262-1	---	---	23,E	23,E	23,E	23,E	23,E	23,E	23,E	23,E
262-2	---	---	31,E	31,E	31,E	31,E	31,E	31,E	31,E	31,E
262A-1	9,E	16,E	16,E	16,E	16,E	16,E	16,E	16,A	16,A	37,E
262A-2	16,E	16,E	16,E (Muzzl)	16,E (Muzzl)	16,E	9,E	16,E	16,A	16,A	16,A
262A-3	14,E	21,E	21,E	21,E	21,E	21,E	21,E	21,E	21,E	16,A
262A-4	---	---	---	---	---	14,E	8A,14E, 12M	16,A	16,A	---
263A-2	---	---	---	---	---	---	---	---	26,E	60,E

[a]Archery in unit 61 only until 1986, units 61, 62, and 62A beginning in 1986.
[b]Muzzleloader season only in unit 61.
[c]Muzzleloader or shotgun only.

harvested between 1984 and 1988), suggesting these two possibilities account for few Sand Creek elk.

We modeled the Sand Creek elk winter population size (2,502 average count/0.8 proportion of herd counted = 3,125), composition (22 bulls:100 cows:54 calves), and harvest to reflect averages from Oldenburg et al. (1980a-1988a, Tables 13-16). If the average estimated harvest between 1980 and 1987 (excluding the 1988 high) of 958 animals (313 2+-year-old bulls, 312 yearling bulls or spikes, 78 yearling cows, 235 adult cows, and an estimated 20 calves) from all hunts is deducted each year, the bull:cow ratio immediately drops to near zero and the number of adult bulls (2+ years old = branch-antlered bulls (BAB)) drops below zero after two seasons. For example, 211 BAB + 180 spikes, recruited to BAB before hunt, yields 391 BAB, with an estimated 313 harvested. Recruitment from calf to spike would yield a maximum of 479 spikes prehunt, of which 312 were harvested leaving 167 available to recruit into the BAB class next year, if all survived. The next year only 78 + 167 BAB would be available for harvest.

The harvest and population estimates do not relate well. Possible reasons for this:

1) population estimates are too low;

2) herd composition counts (bull:cow or calf:cow ratios) are inaccurate due to underestimates of bulls. Models using a population size of 3,100 animals and various spring precalving ratios as high as 50 bulls:100 cows:70 calves, still did not support the estimated average harvest; or

3) the estimate of harvest is incorrect. Estimated harvest confidence intervals for 1987 and 1988 (Table 19) were $\pm$ 325 in 1987 and $\pm$ 387 in 1988;

4) elk harvested in Idaho may have come from Montana since there have been tagged Montana elk killed in Idaho. These elk may come from the Gravelly Range, or areas closer to Sand Creek. In 1987, approximately 2,000 elk wintered in the Wall Creek Game Range of Montana, some of which may summer in Idaho. These animals would most likely be harvested in Idaho units 60 and 61. It is unknown what proportion of the Sand Creek elk harvest came from animals that wintered in Montana. Some Idaho elk moved to Montana (Brown 1985) or were killed in Montana (Idaho Dept. Fish & Game tagging returns), and we thus assumed that immigration equals emigration for our models; or

5) not all elk that contribute to the harvest winter on the Sand Creek winter range. Elk may winter in other areas (e.g., Jackson, Teton River, Fall River, Big Bend Ridge) and make the entire population that is hunted larger than that counted on the Sand Creek winter range. An estimated additional 800-1,000 elk summer and are harvested in the area of the Sand Creek herd, but do not winter on the Sand Creek winter range (J. Naderman pers. comm.).

Table 19. Estimated 1987 and 1988 elk harvest and 95% confidence intervals derived from telephone survey for general and controlled hunts (Nelson 1988, 1989).

Hunt	Hunt Unit	1987 Harvest	1987 95% C.I.	1988 Harvest	1988 95% C.I.
General	60	191	115-267	253	167-339
General	61	250	164-336	309	216-403
General	62	42	7- 77	80	30-130
General	62A	25	0- 53	45	11- 80
Controlled	260-1	66	40- 92	---	---
Controlled	260-2	71	54- 87	---	---
Controlled	260	---	---	271	228-314
Controlled	260A	---	---	60	48- 72
Controlled	262-1	21	14- 27	40	35- 46
Controlled	262-2	49	34- 64	116	102-131
Controlled	262A-1	14	10- 17	34	27- 41
Controlled	262A-2	37	32- 42	41	35- 48
Controlled	262A-3	96	72-120	111	85-138
Controlled	262A-4	30	26- 34	51	46- 57
Controlled	263A-2	---	---	13	12- 15
Total		892	568-1216	1424	1042-1814

We assumed that harvest was the most accurate estimate of the five potential sources of error, and allowed the herd composition to vary slightly from observed averages for our models. Models were run until a population size was found that supported a harvest of 958 elk. The results indicated that the Sand Creek elk herd in spring prior to calving had to be at le[illegible] 4,200 animals (Table 20). Spring precalving herd composition at stable age distribution and finite rate of increase of 1.0 was 27 bulls:100 cows:57 calves. Yearling bull:adult ratio was nearly equal and yearling cows were about 22% of total cows. Survival rates excluding hunting mortality were 0.70-0.75 for calves, 0.86-0.87 for cows, and 0.95-0.96 for bulls (Table 20). Cow reproductive rates were between 0.2 and 0.4 for yearlings and 0.92 and 0.97 for 2+-year-olds. Model parameters for one scenario, assuming a spring precalving population size of approximately 4,300 elk with a summer prehunt population of 5,720 are in Table 20. Harvest rate of calves was 1%, yearling cows 12%, adult cows 10%, yearling bulls 48%, and adult bulls 50% of the summer prehunt population. Although our model population was larger than that estimated on the Sand Creek winter range, the entire population that contributed to the harvest may be closer to our estimates. The estimate of the number of elk that are on the Sand Creek winter range is probably accurate, and the additional animals that contributed to the hunter harvest winter in areas other than the Sand Creek winter range (2,500 average / 0.8 of herd counted + 1,000 that summer in other areas = 4,125, near our estimate of 4,300).

Our models required low cow survival with high bull and calf survival rates and high cow reproductive rates. Recruitment had to be large in order to sustain the heavy harvest of bulls. Cow survival was low to allow bull:cow and calf:cow ratios to approach those observed and keep the population from increasing. These survival rates were not anticipated. A population size larger than 4,300 would give the desired harvest and a lower bull:cow ratio, but with lower survival rates to yield a stable population. Survival rates determined from the age-structure data of cows 2.5+ years old was 0.7329 and of bulls 2.5 years old and older was 0.5228 (Oldenburg 1983a, Table 14). These rates included hunting mortality. If we assume a summer prehunt population size of 4,900 at 44 bulls:100 cows:53 calves with 28 yearling cows:100 2+-year-old cows (Table 20) with adult cow harvest of 235 animals for 1980-1982, then the harvest rate was 0.12 and natural survival rate of 2+-year-old cows was 0.83 (0.7329/(1.0-(235/(.395 x 4,900)), close to our results. We conclude that the greatest unknown with the Sand Creek elk herd is population size from which the hunter harvest is taken.

The impact of wolf predation on Sand Creek elk was modeled in two ways for the balance models. One method was to focus only on elk within southwest Yellowstone National Park during summer, assuming that wolves would not be tolerated outside the park (YNP only scenario). The second approach was to model a broader area, including Yellowstone National Park and areas adjacent to southwest Yellowstone, generally east of U.S. Highway 20 but also including Harriman State Park and the Big Bend Ridge area (BROAD scenario).

Table 20. Sand Creek elk herd model population characteristics. Entire herd modeled for stability.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	661	959	767	757
yrl cows	507	661	641	563
2+ cows	1824	2331	2261	2026
M calves	661	959	767	757
yrl bulls	328	661	654	342
2+ bulls	308	636	630	317
Total	4289	6207	5720	4762
Composition				
bulls:100 cows	27	43	44	26
calves:100 cows	57	64	53	59
yrl cow:100 2+ cow	28	28	28	28
yrl bull:100 2+ bull	106	104	104	108

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.80	0.88	0.70
yrl cows	0.97	0.89	0.86
2+ cows	0.97	0.90	0.87
M calves	0.80	0.88	0.70
yrl bulls	0.99	0.96	0.95
2+ bulls	0.99	0.97	0.96
Fecundity rates			
yrl cows	0.33		
2+ cows	0.96		

Harvest		Harvest rates
F calves	10	10/767 = 0.013
yrl cows	78	78/641 = 0.122
2+ cows	235	235/2261= 0.104
M calves	10	10/767 = 0.013
yrl bulls	312	312/654 = 0.477
2+ bulls	313	313/630 = 0.497
Total	958	

[a]Spring pre-calving is in late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Predation on elk for the BROAD scenario would occur through summer until fall migration. The BROAD scenario would permit wolves to exist in additional forested areas.

Sand Creek Elk Population Characteristics: Leslie Matrix Models

The Leslie matrix model was run until the minimum population that would sustain a hunter harvest of 975 animals of approximate composition represented in the reported estimates of the harvest was obtained. The model population was assumed to be stable at 5,373 elk in winter. Sex ratio stabilized at 39 bulls:100 cows, and age ratio at 77 calves:100 cows. Approximately 46% of the bulls and 13.6% of the cows and calves were harvested from this model population, or 20 calves, 297 yearling bulls, 352 adult bulls, and 307 adult cows. About 46% of the bull harvest was yearlings. Again, we are assuming that the best population data obtained is from the hunter harvest, and we recognize that the population size is higher than trend counts indicate, or that all of the harvested population does not winter in the areas censused.

YNP Scenario: Elk Population Characteristics: Balance Models

The proportion of elk summering in Yellowstone National Park was estimated from collared animal studies of Brown (1985) and Oldenburg et al. (1987a, 1988a, Kuck et al. 1989a). Percentages of collared cow elk in the Yellowstone Plateau and Bechler summer subpopulations were 7.7% and 11.5% respectively (Table 12), or 19.2% total (Brown 1985:95). Brown (1985) produced a variety of estimates of cow elk summering in and adjacent to Yellowstone National Park ranging from 16% to 29%. Between 26% and 40% of radiocollared bull elk summered in Yellowstone with another 5% in units adjacent to the park (Oldenburg et al. 1986a, 1987a, 1988a; Table 21). As the bull study progressed and older animals were collared, a higher percentage of the collared Sand Creek bulls summered in Yellowstone. About 50% of the collared bulls older than 2 years summered in Yellowstone (Oldenburg et al. 1987a, 1988a; Kuck et al. 1989a). We assumed that 27% of the Sand Creek herd summered within Yellowstone National Park for the YNP scenario models. This percentage would vary with changes in hunting regulations and hunting intensity on Yellowstone elk during migrations.

We assumed that harvest from controlled hunt 262A was entirely composed of Yellowstone elk, and added 40% of the average harvest from controlled hunts 260 and 262. Early migration out of Yellowstone National Park or late-rut movements would result in some bull harvest in the general hunt, but this is less predictable than the controlled hunts. Total harvest from animals that summer in Yellowstone was estimated at 219 elk (Table 16: 1980-1987 average controlled hunt harvest Unit 62A = 123 + 40% of 167, Unit 60= 67 + 40% of 73, Unit 62 = 29 = 219) of which 16 were calves of equal sex ratio, 24 yearling bulls, 35 2+-year-old + bulls, 36 yearling cows, and 108 2+-year-old cows. We assumed that 10% of the antlerless harvest were calves. A 25% yearling cow (Table 14) and a 40% yearling bull (Table 15) composition of the cow and bull harvest was used.

We attempted to model the YNP scenario using composition, survival and fecundity rates derived for the entire Sand Creek herd and 27% of 4,300 wintering elk (or 27% of 5,720 elk in summer). Our models could not support the intense cow harvest on the Yellowstone National Park migrants,

Table 21. Proportion of radio-collared bull elk summering in and near Yellowstone National Park (Oldenburg et al. 1985a, 1986a, 1987a).

Date	No. in YNP/ total radio-collared	% in YNP	No. adjacent (62,62A)	% adjacent	Harriman+ Big Bend	%
6/86	5/19	26	0	0	6	32
6/87	10/31	32	2	6	7	23
6/88	8/20	40	1	5	5	25

so different survival and fecundity rates were needed. Calf and cow survival for the YNP scenario was higher (0.73 and 0.96), and bull survival lower (0.71) than the entire herd (Table 22). Higher bull:cow and calf:cow ratios were used than for the entire herd, but the yearling bull:adult bull ratio was lower (Table 22). The proportion of older bulls is probably greater in Yellowstone than for the herd average (Oldenburg et al. 1987a, 1988a). The low bull survival probably includes some harvest of bulls during the general season outside of Yellowstone that we did not explicitly model. It is possible that harvest of calves was higher than our estimated 10% composition of total antlerless harvest, but no supporting data were available. If it was, cow survival rates could be lower than modeled. Additionally, if more than 27% of the herd summers in Yellowstone, or the herd is larger than 4,300 elk in winter, cow survival rates could be lower. Our population size estimate is a minimum number of elk that can support the average controlled hunt harvest from Unit 62A, and 40% of the average controlled hunt harvest from Units 60 and 62, and remain stable. Because model population size, composition, and survival rates were derived from models assuming that harvest was 219 elk, any significant deviation from number harvested or harvest composition would change model parameters.

Our summer prehunt estimate of number of elk from the Sand Creek herd in southwest Yellowstone was 1,555. Using Brown's (1985) data, Singer (1989) estimated that 1,056 Sand Creek, 300 northern range and 70 Madison-Firehole elk were in the Bechler area of Yellowstone during summer. To avoid overestimating the potential impact of wolves on Sand Creek elk, we assumed that wolves would kill elk proportionately and used Singer's (1989) estimates of northern range and Madison herds that summer in southwest Yellowstone to partition the wolf kill (1,555 Sand Creek + 300 northern range + 70 Madison-Firehole) = 0.81 portion of elk killed by wolves would be Sand Creek elk (15% northern elk and Madison-Firehole elk).

BROAD Scenario: Elk Population Characteristics: Balance Models

The second population model assumed wolves would occupy a broader area including the Bechler, Yellowstone Plateau, Caldera, Two Top, Chick Creek, Ashton Hill, and Harriman summer subpopulations (Fig. 7). About 75% of the Sand Creek herd (Table 12), or roughly 4290 elk (0.75 x 5720), were in these areas in late summer. We estimated harvest for the BROAD scenario to come from: 1) entire harvests from general and controlled hunts in Units 62 and 62A; and 2) because about 39% of the elk in Unit 61 summered east of Highway 20, we used this same proportion to estimate harvest from this unit (0.39 x 205 males, 0.39 x 59 females); and 3) an estimated 90% of the general hunt and 80% of the controlled hunt from the Unit 60 harvest. This resulted in a total average harvest of 738 elk, of which 14 were calves, equal sex ratio, 63 yearling cows, 189 adult cows, 236 yearling and 236 adult bulls. Our model population (Table 23) had composition and survival rates similar to the entire Sand Creek herd (Table 20).

Mule Deer Populations

Mule deer that summer in Units 60, and 61, and some deer west of Henry's Fork of the Snake River in Unit 62A migrate to to the Sand Creek winter range in Unit 60A. Some deer that summer in Wyoming may move into Idaho to winter, especially in the Fall River area. There has been no trapping or tagging of deer from Unit 60 winter range since the early 1960s. Trend counts done in Unit 60A on the winter range in December ranged from 1,037 to 1,983 deer between 1982 and 1988 (Kuck et al. 1989, Table 24). Herd composition during winter in Unit 60A averaged 33 bucks:100 does:95 fawns between 1974 and 1988 (Table 24), though this estimate included some deer that summer in Units 62A, 62, 64, and 65. Herd composition in Unit 62 during December averaged 33 bucks:100 does:98 fawns (Oldenburg et al. 1988b). Little information on age structure of the population or harvest has been obtained because few hunters encounter check stations. Management objectives for Units 61, 62, and 62A specified a summer population of 2,400 deer producing a harvest of 420 animals (Trent et al. 1985). The Sands Habitat Management Plan (1978) specified that a winter population of 1,200 in Unit 60A would be maintained.

Harvest in Units 62 and 62A ranged from 41 to 572 animals between 1983 and 1988 (Table 25). The 1984 total harvest was low because of the previous winterkill and the antlerless portion of the hunt was eliminated. The 1988 harvest was high because the antlerless season was longer and the population had probably increased due to mild winters. Effects of the 1988 summer drought and the harsh winter of 1989 resulted in high winter mortality (J. Naderman pers. comm.).

No information on summer population estimates or distribution of deer were available for southwest Yellowstone National Park or Idaho Units 61, 62 and 62A. Singer (1989:51) stated that "a few" deer are present in the Bechler area within Yellowstone during summer and none in winter. During summer, deer tagged on Montana winter ranges have been found in Units 61 and 62A (J. Naderman pers. comm.).

Table 22. Sand Creek elk herd population characteristics: YNP scenario with 27% of entire herd modeled for stability.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	169	246	206	198
yrl cows	129	169	167	131
2+ cows	482	611	605	497
M calves	169	246	206	198
yrl bulls	98	169	159	135
2+ bulls	128	226	212	177
Total	1175	1667	1555	1336
Composition				
bulls:100 cows	37	51	48	50
calves:100 cows	55	63	53	63
yrl cow:100 2+ cow	27	28	28	26
yrl bull:100 2+ bull	77	75	75	76

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.84	0.86	0.72
yrl cows	0.99	0.97	0.96
2+ cows	0.99	0.97	0.96
M calves	0.84	0.86	0.72
yrl bulls	0.94	0.72	0.68
2+ bulls	0.94	0.72	0.68
Fecundity rates			
yrl cows	0.26		
2+ cows	0.95		

Harvest		Harvest rates
F calves	8	8/206 = 0.039
yrl cows	36	36/167 = 0.217
2+ cows	108	108/605 = 0.179
M calves	8	8/206 = 0.039
yrl bulls	24	24/159 = 0.151
2+ bulls	35	35/212 = 0.165
Total	219	

[a]Spring pre-calving is in late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Table 23. Sand Creek elk herd population characteristics: BROAD scenario with 76% of entire herd modeled for stability.

Characteristic	Spring pre-calving[a]	Summer post-calving[b]	Summer pre-hunt[c]	Fall post-hunt[d]
Population				
F calves	497	740	592	579
yrl cows	372	497	482	427
2+ cows	1398	1771	1700	1515
M calves	497	740	592	579
yrl bulls	248	497	492	256
2+ bulls	229	477	472	236
Total	3241	4722	4330	3592
Composition				
bulls:100 cows	27	43	44	25
calves:100 cows	56	65	54	60
yrl cow:100 2+ cow	27	28	28	28
yrl bull:100 2+ bull	108	104	104	108

Survival rates	Summer	Winter	Annual (winter*summer)
F calves	0.80	0.86	0.69
yrl cows	0.97	0.89	0.86
2+ cows	0.96	0.92	0.88
M calves	0.80	0.86	0.69
yrl bulls	0.99	0.97	0.96
2+ bulls	0.99	0.96	0.95
Fecundity rates			
yrl cows	0.33		
2+ cows	0.97		

Harvest		Harvest rates
F calves	13	13/592 = 0.022
yrl cows	55	55/482 = 0.114
2+ cows	185	185/1700= 0.109
M calves	13	13/592 = 0.022
yrl bulls	236	236/492 = 0.480
2+ bulls	236	236/472 = 0.500
Total	738	

[a]Spring pre-calving is in late winter before birthdays.
[b]Summer post-calving is after birthdays, after births, but before summer mortality.
[c]Summer pre-hunt is before hunter harvest and after summer mortality.
[d]Fall post-hunt is after fall harvest but before winter mortality.

Table 24. Mule deer trend and composition data on Junipers area winter range Unit 60A- includes deer from units 60, 61, and 62A and likely others; counts done in December (from Kuck et al. 1989b).

Winter	Count	Buck:Does:Fawns
1979-80	---	65: 100: 91
1980-81	---	65: 100: 92
1981-82	---	61: 100:116
1982-83	1443	---
1983-84	1337	---
1984-85	1983	32: 100: 72
1985-86	1547	29: 100: 96
1986-87	---	37: 100:121
1987-88	---	23: 100:105
1988-89	1684	42: 100: 83
1984-1988 average		33: 100: 95

Table 25. Telephone survey deer harvest estimates from hunt Units 62 and 62A.

	Hunt Unit							
	62				62A			
Year	Doe	Buck	Total	%Mule deer	Doe	Buck	Total	%Mule deer
1983	34	117	151	89	24	47	71	100
1984	0	24	24	100	0	17	17	100
1985	91	54	145	100	0	52	52	100
1986	31	111	142	89	0	64	64	100
1987	116	117	233	100	0	67	67	100
1988	152	308	460	97	12	100	112	78

Population models and impacts of wolves on deer in the southwest portion of Yellowstone and immediate surrounding area should be developed. However, lack of data will affect the accuracy of the estimates. Mule and white-tailed deer (Odocoileus virginianus) will undoubtedly be preyed upon, possibly even preferred over elk (e.g., Carbyn 1975, Carbyn 1983), depending on numbers. How much this will buffer impacts on elk and moose is unknown.

Moose Populations

During winter moose were distributed on five winter ranges associated with the Sand Creek elk herd summer range (Ritchie 1978) which are Junipers (390 km^2, snow depths < 60 cm), Big Bend Ridge (210 km^2, snow depths 76-183 cm), Fall River Ridge (450 km^2, snow depths > 107 cm), Shotgun Valley, and Island Park. Trend counts since 1951 decreased in the 1960s and 1970s with an increase in the 1980s (Table 26). No trend count was made between 1983 and 1987. Average composition between 1969 and 1975 was 70 bulls:100 cows:62 calves with a 12% twinning rate (Ritchie 1978). Incidental observations of moose on the Junipers winter range during 1987-1988 resulted in ratios of 48 bulls:100 cows:56 calves, and in 1988-1989 the ratios were 79:100:43 (Kuck et al. 1989c).

Moose that winter along Fall River are distributed widely in summer, with some in southwest Yellowstone National Park. Their distribution in summer was 12% in Island Park, 32% in Fall River Ridge, and 56% in Wyoming (Ritchie 1978). Wyoming Fish & Game stated that 15% of Idaho moose summer in Wyoming and of these 39% were in Yellowstone (Lockman et al. 1989:424). Moose that summer on the northwest slope of the Teton Range in Wyoming winter in Idaho. Roughly 50% of Fall River Ridge moose summer in Wyoming and of these, more than half are in Yellowstone. Moose that winter in the Junipers and Big Bend Ridge area did not summer in Yellowstone (Ritchie 1978). Moose that winter along Big Bend Ridge may be preyed upon in winter if wolves are allowed outside of Yellowstone.

The Idaho moose harvest in this area was closed from 1977 to 1982, and was reopened for controlled hunts in 1983. Twenty bull-only permits distributed equally among four controlled hunts in Units 62 and 62A have been issued annually, with nearly 100% success. Indian harvest during 1983-1987 averaged 1.8/year for Units 62 and 62A combined. The harvest in Wyoming moose hunt Area 37, adjacent to Yellowstone National Park and Idaho, was 25 in 1988. Harvest in Units 60, 60A, and 61 were probably animals from Junipers and Big Bend Ridge winter ranges; harvest in Units 62, 62A, and Wyoming were likely moose from the Fall River Ridge winter range.

Table 26. Winter trend counts of moose on Idaho winter ranges (Oldenburg and Turner 1989).

Winter	Junipers & Big Bend	Fall River Ridge	Island Park	Total
1951-52	400	153	124	677
1952-53	241	135	133	509
1955-56	270	152	177	599
1957-58	173	92	65	330
1962-63	148	66	68	282
1968-69	126	40	66	232
1972-73	86	69	22	177
1975-76	90	109	74	273
1980-81	172	151	65	388
1981-82	136	159	66	361
1982-83	353	138	61	552
1988-89	339	139	77	555

During the early winter of 1988, Wyoming Fish & Game classified 154 moose on winter ranges of the Targhee Herd (Areas 37 and 16), with 69% of those in Idaho. The posthunt population estimate was 325 with 65 bulls:100 cows:49 calves and 49 adult males:100 cows and 17 yearling males:100 cows (Lockman et al. 1989). The management objective for the Wyoming Targhee herd is a posthunt population of 300 with 60 bulls:100 cows supporting a harvest of 55 moose.

Enough information is known to model moose-wolf dynamics in this area. Population size and composition data, however, are needed in southwest Yellowstone National Park. Moose may not be preferred prey for wolves in Yellowstone during summer. Moose might sustain wolves during winter in the Big Bend and Fall River Ridge areas if wolves are permitted outside of Yellowstone.

Beaver Populations

Because wolf predation on beaver has been documented during summer (Voight et al. 1976), beaver numbers and distribution in and adjacent to southwest Yellowstone National Park should be considered as they might buffer predation on elk, deer, and moose. However, few data are available on beaver populations. Idaho Department of Fish and Game biennial beaver colony counts done in 1985 resulted in a Region 6 average of 1.2 stream miles/colony (Johnson, 1986). Good habitat averaged 1.2, fair 1.8, and poor 2.8 stream miles/colony (Johnson 1986). Average counts between 1967 and 1985 along Rock Creek and Partridge Creek, both adjacent to southwest Yellowstone, averaged 1.3 and 1.6 stream miles/colony respectively (Johnson 1986).

Within southwest Yellowstone, there are three beaver producing streams in the Bechler area: Boundary Creek, Bechler River, and Wyoming Creek (S. Consolo pers. comm.). Beaver habitat is poorer in southwest Yellowstone than outside the park. No estimate on number of active colonies or number of beavers is currently available. Work is being done to further estimate beaver numbers and distribution in Yellowstone National Park (Consolo and Hanson 1990).

Deer, moose, and beaver populations may buffer wolf impacts on elk by providing alternate prey. We did not explicitly model these potential alternate prey, but recognized that they might be important. We reduced wolf predation on elk for all of the models by what we felt might be reduced due to their use of a alternate prey.

Aspects of Wolf Predation on Sand Creek Elk

For the YNP scenario we assumed that wolves would prey on elk during summer and fall and then migrate to either the upper Snake River or Madison-Firehole areas of Yellowstone National Park. Since wolves have their pups in April, they would not be able to migrate until late June after the pups were older. This would reduce the amount of time that wolves preyed on elk in early

summer during calving. Brown (1985) determined the length of stay on the summer range by radiocollared elk (Table 11). The amount of time varied with animal, subpopulation, and weather. Brown (1985) estimated that the median time spent on the summer range was 138 days for elk not using Harriman State Park and 168 days for those using it. For the YNP scenario we assumed that elk were vulnerable to predation by wolves for 150 days. For the BROAD scenario we assumed that wolves would prey on elk during summer and early fall and then either migrate to the upper Snake River, or Madison-Firehole areas of Yellowstone, or spend winter on Big Bend Ridge preying on moose and the few elk that winter there. We used 180 days (mid-May through mid-November) spent by elk on summer range and vulnerable to predation by wolves for the BROAD model.

The LOW, MODERATE, and HIGH kill rates by wolves on elk were again used (Table 27). Predation rates on Sand Creek elk for the YNP scenario were derived by assuming summer was 150 days, 90% of the diet by biomass were elk, and 85% of the elk were from the Sand Creek herd. The LOW scenario requirement was estimated at 287 kg/wolf of Sand Creek elk (1.9 kg elk/wolf/day), and resulted in 3.2 Sand Creek elk killed/wolf during summer (Table 27). The MODERATE scenario requirement was estimated at 585 kg/wolf of Sand Creek elk (3.9 kg/wolf/day), or 6.7 Sand Creek elk killed/wolf. For the HIGH scenario, an estimated 8 Sand Creek elk killed/wolf was used (150 days vulnerable to predation / 365 x 28 ungulates/wolf/year = 12 ungulates x 0.8 proportion of ungulates killed are elk = 10 elk x 0.8 proportion of elk in southwest YNP that are Sand Creek elk = 8 Sand Creek elk/wolf preyed upon during summer). Consumption rate for the HIGH scenario was estimated at 4.8 kg/wolf/day of all prey types, or 3.5 kg/wolf/day of Sand Creek elk only (Table 27).

The estimate for the BROAD scenario at LOW predation was 180 days x 2.5 kg/wolf/day x 0.85 of diet consists of elk x 0.95 elk are Sand Creek elk = 363 kg elk, or 2.0 kg/wolf/day of Sand Creek elk. The estimated kill rate for the LOW scenario was 4.2 elk/wolf (Table 27). The estimated MODERATE consumption was 741 kg, or 4.1 kg/wolf/day of Sand Creek elk (Table 27). The estimated kill rate for the MODERATE scenario was 8.6 elk/wolf. An estimated 10 elk killed/wolf was used for the HIGH model (180 days vulnerable to predation / 365 x 28 ungulates/wolf/year = 14 ungulates x 0.7 proportion of ungulates are elk (because more deer and moose occur outside of YNP) = 10 elk /wolf). Consumption rate for this model was estimated at 5.6 kg/wolf/day of all prey types, or 4.1 kg/wolf/day of Sand Creek elk (Table 27).

Table 27. Distribution of assumed predation, and estimated biomass consumption by wolves on Sand Creek elk, by age and sex, used in the YNP and BROAD scenario models. LOW, MODERATE, and HIGH kill rates are presented.

Scenario Sex-age	Number of elk killed/wolf LOW	MODERATE	HIGH	Utilization	Mass of prey (kg)	Consumption (kg/wolf) LOW	MODERATE	HIGH
YNP scenario (150 days)								
Female								
calves	0.95	2.0	3.0	0.80	30	23	48	72
yearling	0.13	0.27	0.2	0.75	240	23	49	36
2+ cows	0.52	1.08	0.8	0.75	240	94	194	144
Male								
calves	0.95	2.0	3.0	0.80	30	23	48	72
yearling	0.28	0.58	0.4	0.75	260	55	113	78
2+ bulls	0.37	0.77	0.6	0.75	260	72	150	117
Total	3.2	6.7	8.0			290	602	519
BROAD scenario (180 days)								
Female								
calves	1.25	2.6	3.5	0.80	30	30	62	84
yearling	0.16	0.32	0.3	0.75	240	29	58	54
2+ cows	0.64	1.28	1.2	0.75	240	115	230	216
Male								
calves	1.25	2.6	3.5	0.75	30	30	62	84
yearling	0.46	0.92	0.75[a]	0.75	260	90	179	146
2+ bulls	0.44	0.88	0.75[d]	0.75	260	86	172	146
Total	4.2	8.6	10.0			380	763	730

[a]Includes 0.5 killed pre-hunt and 0.25 killed post-hunt by wolves.

Predation rates for the Leslie matrix models were shown in Table 9. We assumed elk would comprise either 75% of 12 ungulates (low) or 90% of 28 ungulates (high) killed/year/wolf. Leslie matrix projections of predation on the Sand Creek elk herd were applied to the entire herd year-round.

Predation was modeled as occurring equally across the entire range of elk for the area modeled. Few geographic barriers exist in southwest Yellowstone or in the BROAD scenario area that would restrict movements of wolves.

Methods of Applying Wolf Predation to Sand Creek Elk Balance Models

As with the Gallatin balance models, two methods of simulating predation were used. One method used constant survival, fecundity, harvest, and predation rates for the population with a range of wolf numbers. The second method explored varying harvest rates, which managers can control, to explore a range of harvest strategies. The YNP scenario examined calf harvest rates ranging from 1% to 10%, cow harvest 10 to 25%, and bull harvest 10% to 40% of the prehunt population (4960 different scenarios). The BROAD scenario examined calf harvest rates ranging from 1% to 10%, cow harvest from 5% to 20%, and bull harvest from 25% to 60% of the prehunt population (5,760 different scenarios). For each of these methods the LOW, MODERATE, and HIGH kill rates were applied. With the variable harvest models, more than 15,000 different scenarios were run for each individual wolf, or 300,000 runs for a range of 1 to 20 wolves for each the YNP and BROAD scenarios.

Wolf Predation on Sand Creek Elk: YNP Scenario Using Balance Models

Output from the YNP model assuming constant survival, fecundity, and harvest rates (Table 22) for the LOW and MODERATE kill rates (Table 27) over five years is shown in Fig. 11. Since our models were derived from average harvest and assumed stable populations, any additional mortality caused a population decline (Figs. 11a and 11b) and harvest decline (Figs. 11c and 11d). With more wolves, the decline in population size and harvest became more rapid. The short-term impacts of constant wolf predation were minimal, but were increased with time. This type model assumed no change in harvest composition, something managers can control. Managers would likely respond to changes in population size by temporarily restricting harvest to allow populations to rebuild, resulting in population fluctuations around a stable mean. If prey populations decline considerably it is unlikely that wolves would remain in an area unless an adequate alternate prey base was available. If alternative prey supported a large wolf population after a principle prey decline, then the principle prey population could be held at a low "equilibrium". But if wolves died or moved out of an area, prey populations would rebound if harvest and weather were favorable. Disturbances such as drought or winterkill might be additive to wolf predation and result in steeper declines than shown in Fig. 11. Mild weather, use of alternative prey, wolf declines or good forage conditions, however, would buffer the impacts of wolf predation.

The models of variable harvest rates with constant survival, fecundity (Table 22), and predation rates (Table 27) showed that a range of harvest could be obtained for a set number of wolves (Fig. 12). Graphs shown are for stable elk populations experiencing constant wolf predation for 15 years with LOW, MODERATE, and HIGH kill rates. The range of harvest was due to examining different combinations of harvest rates for different sex/age classes.

Higher elk harvests in the presence of wolf predation could be obtained by reducing cow harvest and increasing the percent of total harvest obtained from bulls (Fig. 13). Our population analysis of the Yellowstone portion of the Sand Creek herd indicated that bull:cow ratios were higher than for the entire herd, and natural cow survival rates (excluding hunter harvest) were very high. This would suggest that cows migrating from Yellowstone National Park were being intensively harvested, but that bulls from Yellowstone were not as heavily harvested as other portions of the Sand Creek population. If additional harvest of migrating bulls from Yellowstone occurred, pressure on bulls in the rest of the population could be reduced. The reduction in antlerless (cow+calf) harvest over a range of wolf numbers for LOW and MODERATE kill rates are shown (Fig. 14). If cow elk were killed in proportion to their occurrence in the population, rather than the estimated proportions used (Table 27), then cow harvest reductions greater than those projected in these models would be required, and total harvest would be less than projected.

The models suggested that with 10 adult wolves preying on elk only during summer, the Yellowstone National Park portion of the Sand Creek herd (1,555 elk in late summer) could be stable, and could support an average annual harvest between 170 and 270 elk (Fig. 12), with no change in survival rates. Harvest of antlerless elk must drop to between 14% and 16%, and bull harvest could be more than 30% of the late-summer prehunt population. Disturbances such as drought or winterkill might be additive to wolf predation and result in a lower harvest than shown in Fig. 12. Mild weather and good forage conditions, however, could produce an increasing population that could support more wolves or higher harvest. Increased predation on alternative prey would buffer wolf impacts on Sand Creek elk. Compensatory (density-dependent) responses such as increased calf survival or increased yearling fecundity by elk would result in greater production, yielding more elk for harvest or supporting more wolves. However, compensatory responses in reproduction are unlikely to occur in the Sand Creek herd because it is heavily hunted and is probably at maximum productivity.

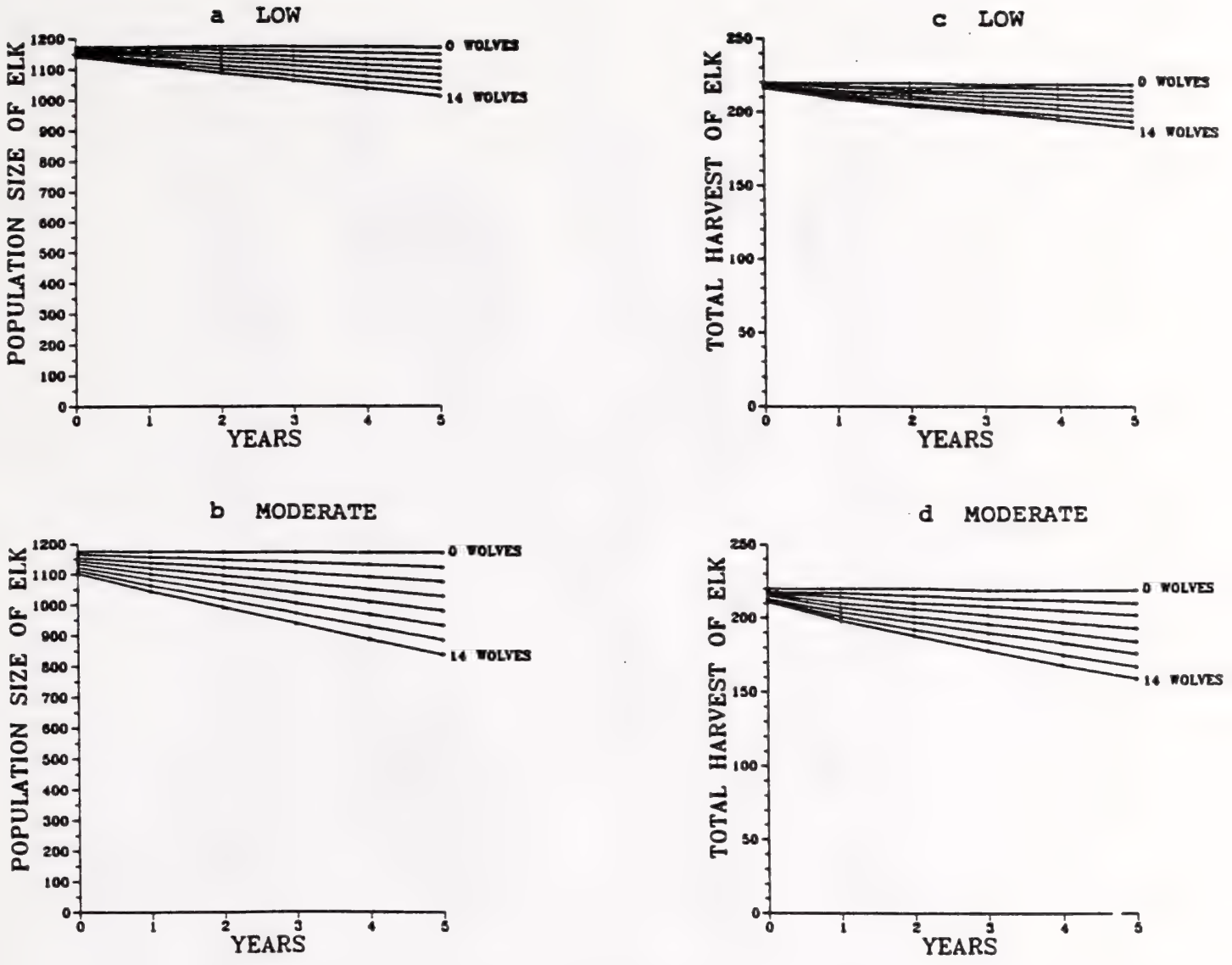

Fig. 11. Potential initial 5-year wolf restoration impacts on the Sand Creek elk herd, YNP scenario, population size (a,b) and total hunter harvest of elk (c,d). Models assume no changes in elk management, or wolf numbers, distribution, or behavior. LOW (a,c) and MODERATE (b,d) wolf kill rates are presented.

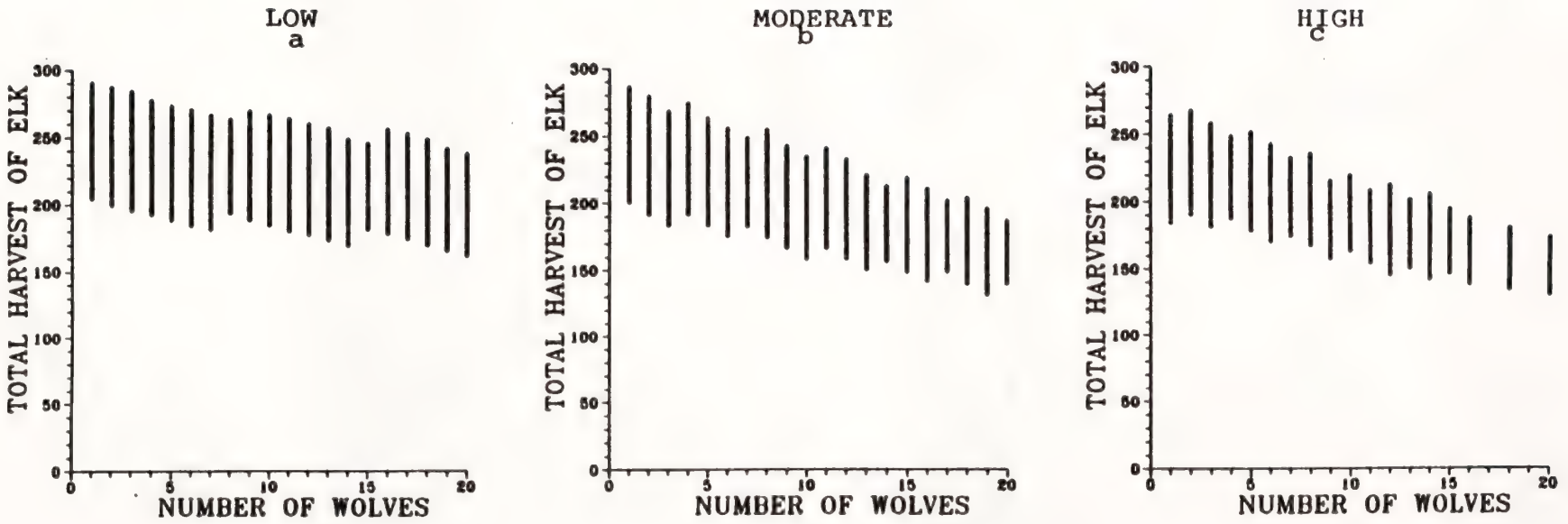

Fig. 12. Range in potential total hunter harvest of elk related to number of wolves for the LOW (a), MODERATE (b), and HIGH (c) kill rates evaluated for the Sand Creek YNP scenario. Range in total harvest results from examining many sex/age combinations of hunter harvest rates.

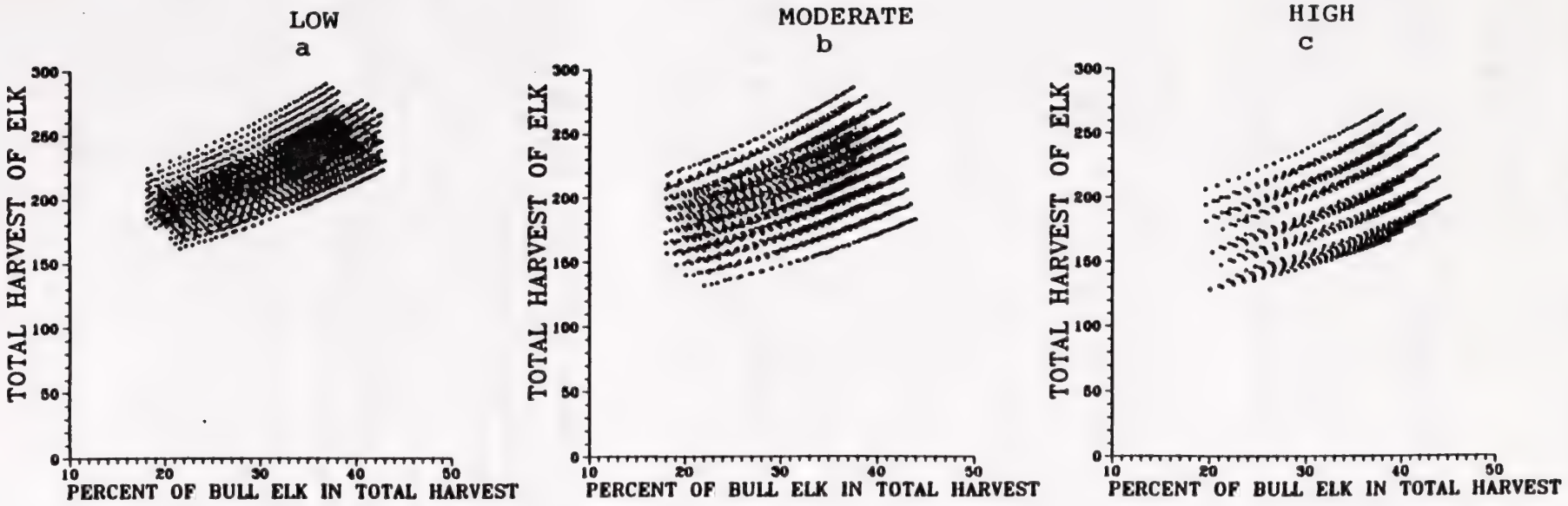

Fig. 13. Range in potentail total hunter harvest of elk related to percent of bulls in total harvest for the LOW (a), MODERATE (b), and HIGH (c) kill rate scenarios evaluated for the Sand Creek YNP scenario. Ranges in total harvest relate to the range of wolves shown in Fig. 12.

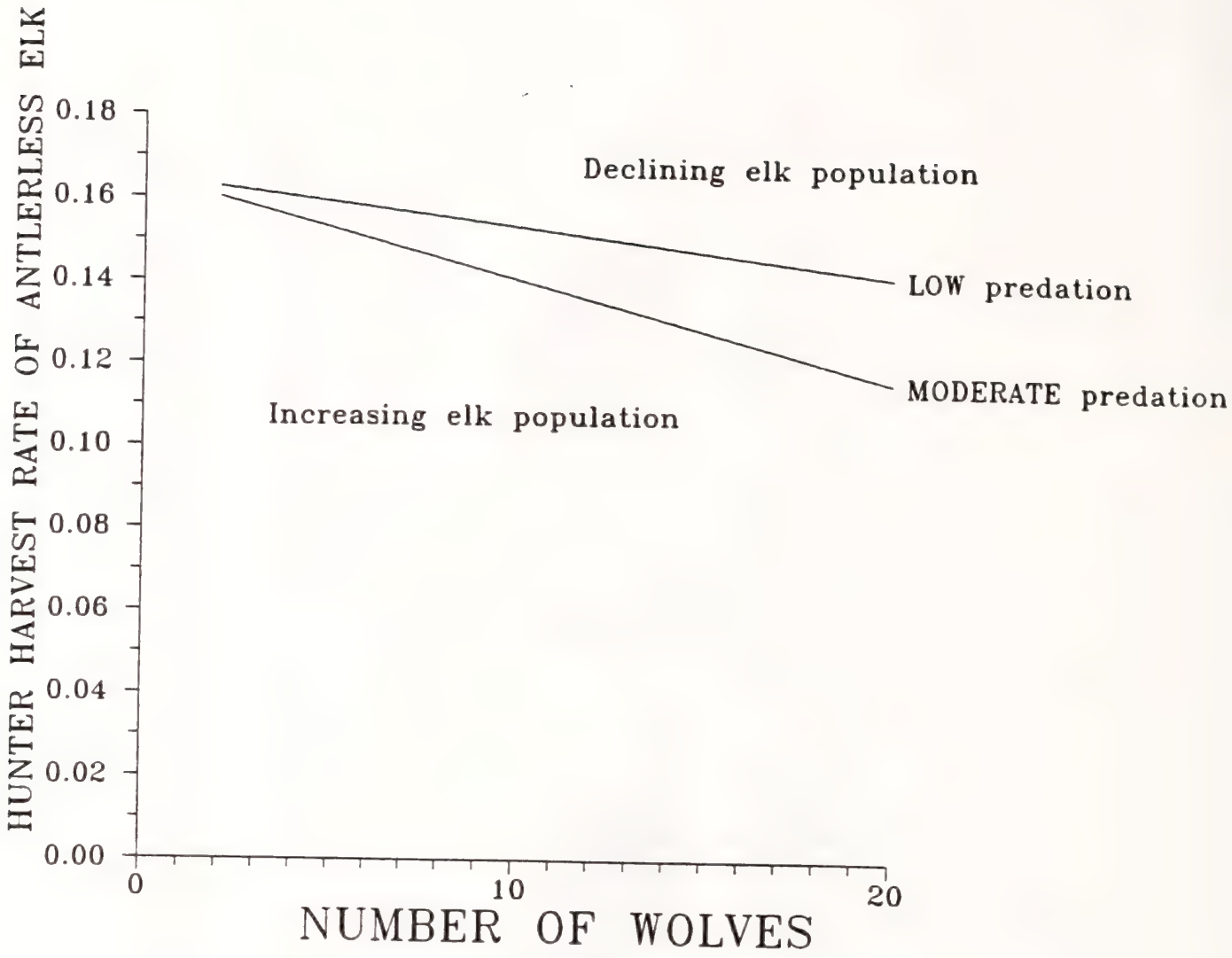

Fig. 14. Change in hunter harvest rate of antlerless elk needed to maintain a stable population at varying number of wolves for the LOW and MODERATE kill rates evaluated in the Sand Creek YNP scenario. Harvest rates below lines result in increasing populations; harvest rates above result in declining populations, with no change in survival or fecundity. Region of uncertainty exists between lines: harvest rate will be dependent upon wolf response and predation rate on elk.

Wolf Predation on Sand Creek Elk: BROAD Scenario Using Balance Models

Results of the model for the BROAD scenario assuming constant survival, fecundity, and harvest (Table 23), with LOW and MODERATE kill rates (Table 27) over five years are shown in Fig. 15. Like the YNP scenario, our models were derived from average harvest and assumed stable populations with wolf predation being equally distributed across the area modeled. Population size (Figs. 15a and 15b) and harvest (Figs. 15c and 15d) declined with added mortality from wolf predation.

The BROAD scenario models with variable hunter harvest rates assumed constant survival and fecundity (Table 23), and used the LOW, MODERATE kill rates (Table 27). Model results were for stable populations experiencing constant wolf predation for 15 years. Output in Fig. 16 showed a narrower range of harvest possible for a given level of wolf predation than the YNP scenario on a percentage basis. The narrower range resulted from the Sand Creek herd already producing maximum bull harvest with little opportunity to increase or maintain harvest by increasing bull harvest rate. With an increasing number of wolves, the cow harvest rate must decrease to maintain stable populations, and thus total harvest declines. In this scenario, highest harvests were reached by increasing the cow contribution to the total harvest. As bulls became a larger fraction of the total harvest, total harvest declined (Fig. 17). High total harvest could be maintained by slightly increasing the cow fraction of the total harvest, but hunting pressure should be on cows other than those migrating from YNP. Management options like manipulating hunter harvest provide few opportunities to support a substantial wolf population and current level of hunter harvest. The results of this model assumed that our guesses at population size and harvest in these areas are correct.

The BROAD scenario models suggested that this portion of the Sand Creek herd (4,354 elk in late summer) could be stable, support an average annual hunter harvest between 640 and 770 elk, depending on intensity of predation, and support 10 adult wolves (Fig. 16) over 180 days with no change in survival rates.

Wolf Predation on Sand Creek Elk: Leslie Matrix Models

Leslie matrix projections were run only on the entire Sand Creek herd scenario. Wolf predation is incorporated into this model by adjusting annual survival rates downward by the amount specified in Table 9. The age/sex specific proportion of the population taken per wolf per year is multiplied by the number of wolves and then subtracted from the annual survival rate.

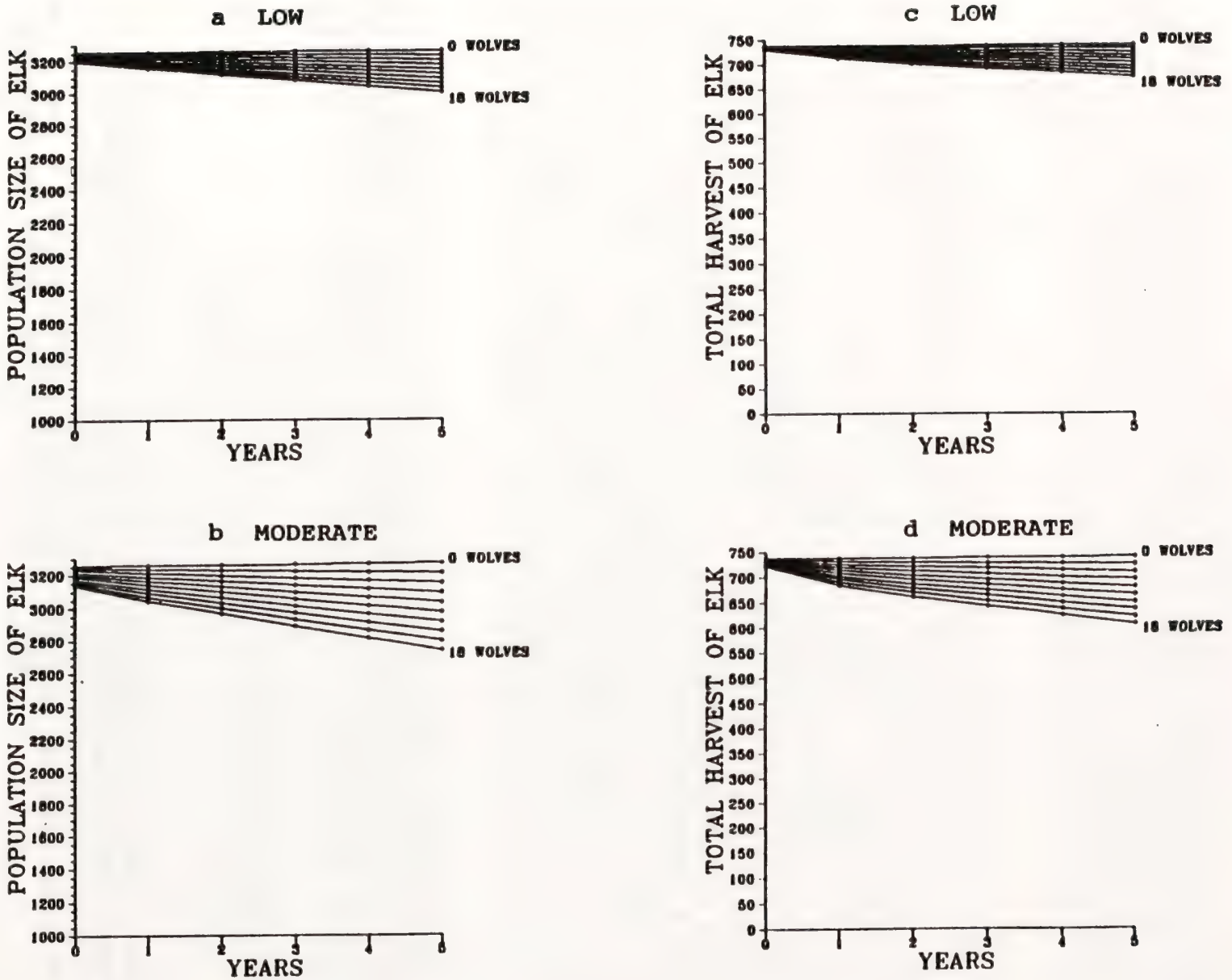

Fig. 15. Potential initial 5-year wolf restoration impacts on the Sand Creek elk herd, BROAD scenario, population size (a,b) and total hunter harvest of elk (c,d). Models assume no changes in elk management, or wolf numbers, distribution, or behavior. LOW (a,c) and MODERATE (b,d) wolf kill rates are presented.

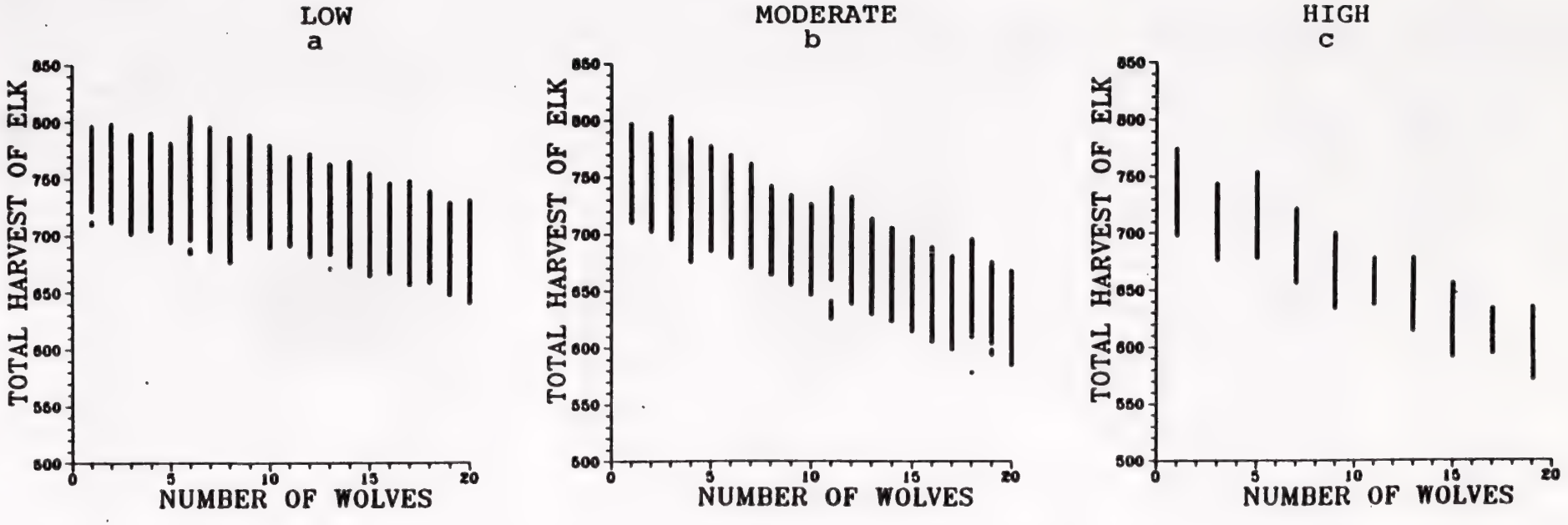

Fig. 16. Range in potential total hunter harvest of elk related to number of wolves for the LOW (a), MODERATE (b), and HIGH (c) kill rates evaluated for the Sand Creek BROAD scenario. Range in total harvest results from examining many sex/age combinations of hunter harvest rates.

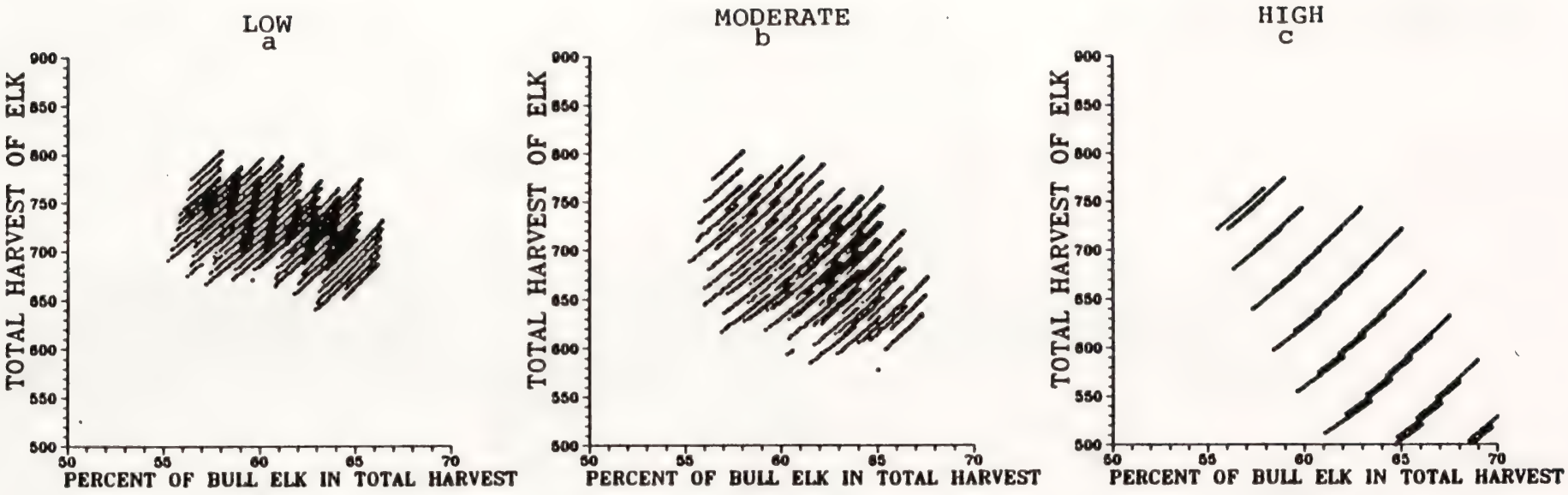

Fig. 17. Range in potential total hunter harvest of elk related to percent of bulls in total harvest for the LOW (a), MODERATE (b), and HIGH (c) kill rate scenarios evaluated for the Sand Creek BROAD scenario. Ranges in total harvest relate to the range of wolves shown in Fig. 16.

The low and high ranges of predation assume that elk constitute 75% of 12 ungulates killed/wolf/year and 90% of 28 ungulates killed/wolf/year for a range in predation of 9-25 killed/wolf/year.

When the hunter harvest is set at the average for the 1980-1987 period of 975 elk, the population drops with either high or low levels of predation, with either 10 or 20 wolves present (Table 28). However, when hunter harvest is constrained to bulls only, then finite rates suggest that population increases would occur in the presence of up to 30 wolves (Table 28). These data suggest that if wolves were kept below 30, some antlerless harvest on the entire population could be allowed, assuming that the goal of management is to keep the population stable.

DISCUSSION

Our models suggest that a reduction in harvest on both the Gallatin and Sand Creek elk herds would be needed in the presence of wolves if no population increase, compensatory response in diminished mortality from other causes, or increased survival was to occur. The reduction would be less than our estimates if wolf predation rates are lower than we used in the models. Disturbances such as drought or winterkill might be additive to wolf predation and require lower harvests than shown in Figs. 4, 12 and 16. Mild weather and good forage conditions, however, could produce an increasing population that could support more wolves or higher harvest. Compensatory (density-dependent) responses such as increased calf survival or increased yearling fecundity by elk would result in greater production which would yield more elk for harvest or allow more wolves to be present. As we suggested for the East Front (Peek and Vales 1989), the need to investigate compensatory responses in prey populations when wolves begin to exert significant predation is especially critical.

The Leslie matrix and balance models were basically similar, though the balance models were used to examine many different hunter harvest regimes. Differences between the models in output were due more to differences in estimating numbers of prey killed and predation partitioning among sex/age classes than model structural differences.

Both the Gallatin and Sand Creek elk herds have special hunts to keep the population within predetermined limits. Hunter harvest is high, especially on females, in order to reach these goals. Our models were built on the current average conditions. Once populations are reduced to reach the desired goal, special hunts and antlerless harvests would most likely be reduced to prevent further declines in the population. In this event, harvest and population size would likely be lower than we modeled here. Because the purpose of special hunts is to manage population sizes, wolf predation could substitute for some of the removal attributed to special hunts and help keep populations at desired levels.

Table 28. Rates of increase of the model Sand Creek elk population with different levels of wolf predation, with and without antlerless harvest. Low level of wolf predation specify 9 elk killed; high level 25 elk killed. Predation is modeled as occurring on the entire Sand Creek herd year-round.

Hunter harvest	Number of wolves	Level of wolf predation	Finite rate of increase of elk population
1980-87 level[a]	none	none	1.0005
1980-87 level	10	low	0.9873
1980-87 level	10	high	0.9808
1980-87 level	20	low	0.9641
1980-87 level	20	high	0.9567
No antlerless	20	low	1.0812
No antlerless	20	high	1.0728
No antlerless	30	low	1.0611
No antlerless	30	high	1.0476

[a]Average was 975 elk

Our investigations indicated that more information on actual population size, survival rates, and sex/age composition of these populations will be needed prior to and when wolves are restored to the area. In the presence of wolves, more intensive monitoring of both predator and prey will be needed to quickly respond with management actions to keep hunter harvest and populations at desired levels. Our modeling efforts are considered qualitative rather than strictly quantitative because of the abundance of unknowns involved. In evaluating our models, the assumptions of the models and weaknesses in the data base must be considered. However, the main conclusion is similar to what Peek and Vales (1989) reported for the East Front elk populations, and Van Ballenberghe and Dart (1982) reported for moose in central Alaska: the presence of wolves means that hunter harvest will likely be confined to males most of the time.

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SECTION 4

Predicted Effects of Wolf Restoration

SOME PREDICTIONS CONCERNING A WOLF RECOVERY INTO YELLOWSTONE NATIONAL PARK:

How Wolf Recovery May Affect Park Visitors, Ungulates, and Other Predators

Francis J. Singer
National Park Service
Division of Research
P.O. Box 168
Yellowstone National Park, WY 82190

SOME PREDICTIONS CONCERNING A WOLF RECOVERY INTO YELLOWSTONE NATIONAL PARK: How Wolf Recovery May Affect Park Visitors, Ungulates, and Other Predators

Francis J. Singer, National Park Service, Division of Research,
P.O. Box 168, Yellowstone National Park, WY 82190

EXECUTIVE SUMMARY

1. It is predicted that 7-9 gray wolf (Canis lupus) packs with fixed territories could occupy Yellowstone's northern winter range; another 1-2 packs could occupy the park's other winter ranges, and another 3-4 packs could be supported, but only if the latter packs were migratory or semimigratory. Overall, the park could support 8-11 wolf packs and portions of the territories of another 3-4 packs.

2. Opportunity for park visitors to view wild ungulates could decline slightly after wolf reoccupation of Yellowstone National Park, but viewing of habituated elk (Cervus elaphus), those that frequent developed areas, may increase since wolves will avoid these areas. Even though adult female ungulates with young change their habits due to wolf presence, they are typically shy and infrequently observed by park visitors even in the absence of wolves. Any changes in the distribution or behavior of other adult ungulates and older young are predicted to be minor.

3. The average relative abundance of ungulates on Yellowstone's northern range during the 1980's was 100 elk:10 mule deer (Odocoileus hemionus):2 bison (Bison bison):2 pronghorn (Antilocapra americana):1 bighorn sheep (Ovis canadensis):1 moose (Alces alces). Published studies indicate that the most to least vulnerable ungulates during winter would be pronghorn > bighorn sheep > mule deer > white-tailed deer (Odocoileus virgiana) > elk > bison > moose. However, since few mule deer, pronghorn or white-tailed deer winter within the park, and bighorns occupy steep rocky escape terrain, wolves are predicted to kill ungulates during winter on the northern range as follows: elk > bison > mule deer > moose > pronghorn > bighorn sheep.

4. Ungulates on three other ranges within Yellowstone National Park occur in a ratio of about 100 bison:95 elk:5 moose:1 mule deer. Wolves are predicted to kill ungulates during winter on these other ranges in the following order: elk ≅ bison > moose > mule deer.

5. Young ungulates of all species are vulnerable to wolves during summer. Parkwide ungulate ratios during summer are 100 elk:16+ mule deer: 8 bison:3+ moose:3 bighorn sheep:1 pronghorn:<1 white-tailed deer or

mountain goat (Oreamnos americanus). Wolves are predicted to kill ungulates during summer in the order of most to least: elk > mule deer > bison > moose > bighorn sheep > pronghorn > mountain goat.

6. Wolves may limit the numbers of a more vulnerable, less abundant prey species when wolf numbers are set by a less vulnerable, more abundant prey species. This potential exists for mule deer, pronghorns, and bighorn sheep. Each of these species is substantially less abundant than elk and is more vulnerable to wolves than elk in snow. However, these more vulnerable species are not predicted to be greatly reduced by wolves since mule deer and pronghorn winter near or north of Gardiner, Montana, where sustained pack activity by wolves is unlikely, and bighorn sheep are relatively secure from wolves near steep, cliffy terrain. Moose are of special concern since they are already harvested by humans at high levels on the northern range. White-tailed deer status should change little since whitetails generally occupy areas distant from likely wolf occupation areas. Bison on the northern range should be less vulnerable than other ungulates, but more vulnerable on the Mary Mountain and Pelican winter ranges due to deeper snows in these areas.

7. Yellowstone Park ungulates that winter in scattered thermal areas of a few hectares in size on the plateaus of the park's interior could be vulnerable to wolves since wolves could chase the ungulates into adjacent deep snows. Conversely, ungulates in the larger, relatively snow-free thermal areas should not be as vulnerable to wolves, since they will have more opportunity to outrun wolves.

8. Yellowstone Park's coyotes (Canis latrans) will probably decline and red fox (Vulpes vulpes) will probably increase after wolf recovery. Black bears (Ursus americanus) and wolves usurp carcasses from each other, and wolves occasionally prey upon black bears, but no published information suggests either species would be significantly affected at the population level. Wolverines (Gulo gulo) can be killed by wolves, but they can also escape from wolves by climbing trees which are numerous in Yellowstone Park. Little published information was available on possible competition between wolves and wolverines at carcasses. Minor effects upon grizzly bears (Ursus arctos) and mountain lions (Felis concolor) are predicted.

9. Humans disrupt activity at wolf dens which can cause wolves to move their pups. To avoid this disturbance many parks close the area surrounding wolf dens to human activity. Closures around wolf den sites tend to be smaller in forested habitats than in open areas. Closures vary from 2.6 km^2 in Voyageurs National Park and 13 km^2 in Isle Royale National Park (forested areas) to 41 km^2 in the tundra habitat of Denali National Park. In Yellowstone, den site closures will probably vary from no additional measures for dens in remote forested areas or in existing bear management zones to small closures at more accessible den sites.

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SOME PREDICTIONS CONCERNING A WOLF RECOVERY INTO YELLOWSTONE NATIONAL PARK: How Wolf Recovery may Affect Park Visitors, Ungulates, and Other Predators

Francis J. Singer, National Park Service, Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190

ABSTRACT: Information on ungulate prey populations and dynamics was reviewed and the effects of a possible gray wolf (Canis lupus) reintroduction into Yellowstone National Park are predicted. Approximately 23,800 ungulates winter inside the park, the vast majority of these (19,300, or 81%), occupy the northern range. Average ungulate ratios from 1980 to 1988 were 100 elk:10 mule deer (Odocoileus hemionus):2 bison (Bison bison):2 pronghorn (Antilocapra americana):1 bighorn sheep (Ovis canadensis):1 moose (Alces alces). Based on preference, wolves are predicted to kill ungulates in winter on the northern range in the following order: elk > bison > mule deer > moose > pronghorn > bighorn sheep. However, few mule deer and pronghorn winter within Yellowstone, and bighorn sheep occupy steep, rock escape terrain. Based on relative availability, pronghorn, mule deer and bighorn sheep are not predicted to be major sources of prey for wolves in winter. Ungulate ratios for other winter ranges in Yellowstone were 100 bison:95 elk:5 moose:1 mule deer. In summer, as many as 37,800 ungulates live in the park. Wolves are predicted to kill ungulates in the following order in summer: elk > mule deer > bison > moose > bighorns > pronghorn. Prey distribution and population estimates indicate that 7-9 wolf packs with fixed territories could occupy Yellowstone's northern range, another 1-2 packs could occupy the park's other ranges, and an additional 3-4 packs could be supported if they were semimigratory. Overall, the park could support 11-15 wolf packs. Park visitor opportunities to view wild ungulates could decline slightly after wolf recovery, but the presence of habituated ungulates near human developments should remain the same or increase. Coyote (Canis latrans) populations are predicted to decline, but still be abundant after wolf restoration, populations of red fox (Vulpes vulpes), which are rare in the park, will increase, and effects on wolverines (Gulo gulo) and mountain lions (Felis concolor) cannot be predicted from available data.

On August 15, 1988, the U.S. Congress directed the National Park Service and the U.S. Fish and Wildlife Service to study questions and concerns about the proposed restoration of wolves (Canis lupus) into Yellowstone National Park. The study was to include, but not be limited to, "How a reintroduced population of wolves may affect the prey base in Yellowstone National Park and big game hunting in areas surrounding the park." The reintroduction of wolves may affect other species of predators or scavengers. The park visitor experience might be reduced if viewing opportunities for ungulates were reduced, or if significant portions of parklands were closed to visitor access to protect wolf den sites. The purpose of this paper is to review the published literature and Yellowstone National Park records in an effort to answer the following questions:

1) What would be the prey of wolves?

2) Would wolves affect the demography, population size, distribution, or behavior of park ungulates?

3) How would the park visitor experience be affected?

4) How would other predators be affected?

DESCRIPTION OF STUDY AREAS

Yellowstone National Park

Nearly all of Yellowstone National Park provides summer range for elk (Cervus elaphus) and other ungulates. The park is 79% forested, made up of about 81% lodgepole pine (Pinus contorta) forests between 2,300 m and 2,600 m in elevation (Houston 1982). In summer, elk concentrate near wet meadows, herblands on the higher plateaus, alpine tundra, and a wide variety of forest openings (Meagher 1973, Houston 1982).

The high plateaus and ridges in Yellowstone receive up to 190 cm of precipitation annually, most of which falls as snow. Winter snowfalls force elk and other ungulates to leave most of the park's interior. Wintering ungulates occur on the Madison-Firehole/Mary Mountain, Thorofare, Pelican, and Gallatin winter ranges (Figs. 1 and 2).

Northern Elk Winter Range

Yellowstone's northern elk winter range is defined as the area where elk from the northern Yellowstone herd winter. About 82% of the northern range lies within Yellowstone National Park, and the remaining 18% lies outside of the park on national forest and private lands. Houston (1982) described the area as about 100,000 ha between Silver Gate and Dome Mountain, Montana (Fig. 1). Elevations on the northern range are between 1,500 m and 2,400 m. More ungulates winter in this area than on the higher plateaus of the park's interior (Meagher 1973, Houston 1982). The northern winter range is warmer and drier than the rest of the park (Houston 1982). Precipitation on the northern range varies greatly due to the considerable variation in elevation. Mean annual precipitation is 30 cm near Gardiner, Montana, but 55 cm near the Lamar Ranger Station 35 km uprange. Most of the northern range averages 75 cm or less of total precipitation (P. Farnes, unpubl. data, Houston 1982).

METHODS

The published literature concerning wolves and unpublished government reports of ungulate surveys and counts were reviewed. Ungulate population data provided in Mack et al. (1990), Singer (1990), Meagher (in review) for the years 1980-1988 was summarized. Methodology is described in Meagher (1973, 1989), Houston (1982), Chu et al. (1989), Hurley et al. (1989), Lockman et al. (1989), and Singer (1990).

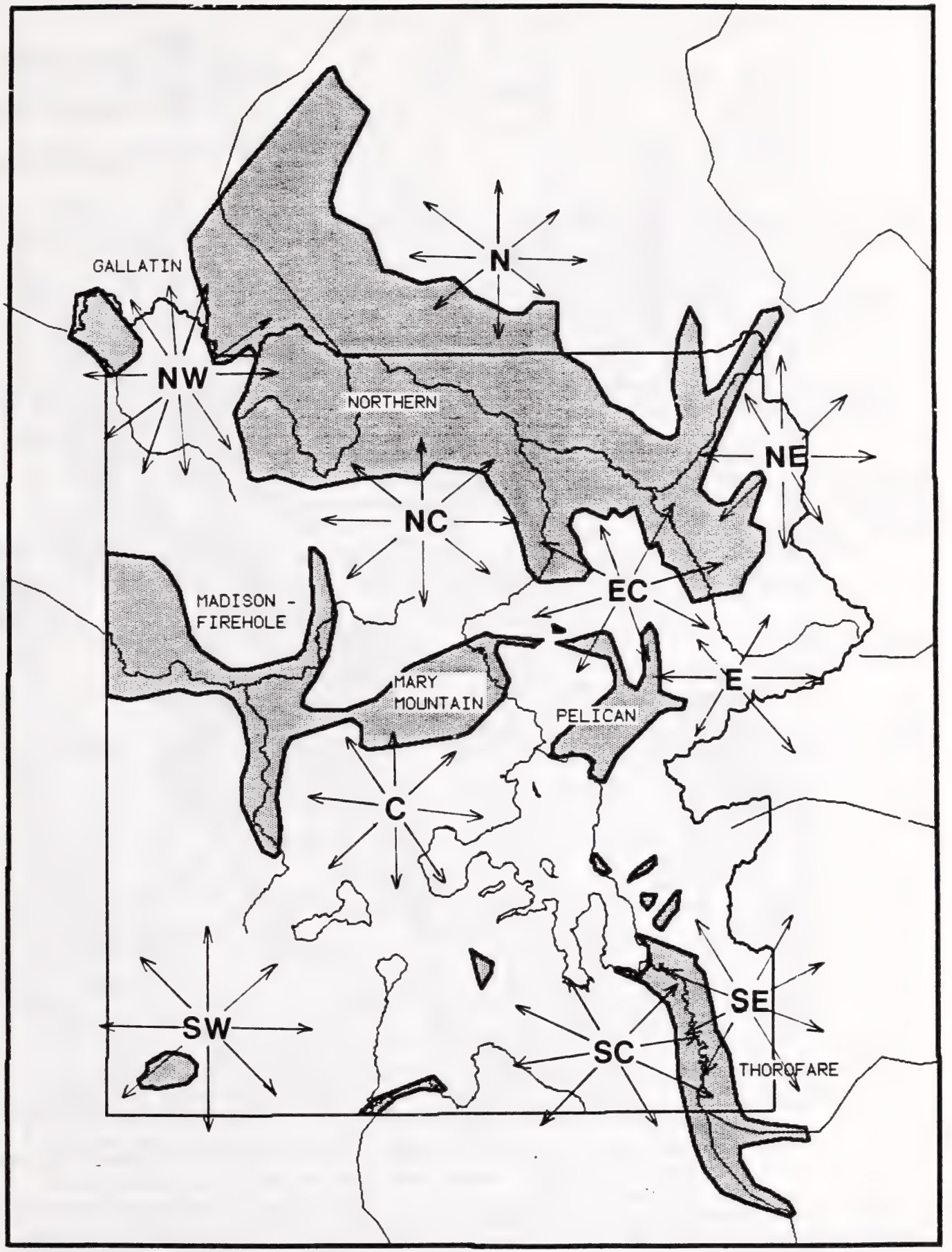


Fig. 1. Winter ranges for ungulates within the boundaries of Yellowstone National Park. The approximate center of 7 major concentrations for elk in summer are marked (NE-northeast, etc.). All of Yellowstone National Park is occupied by some elk during summer.

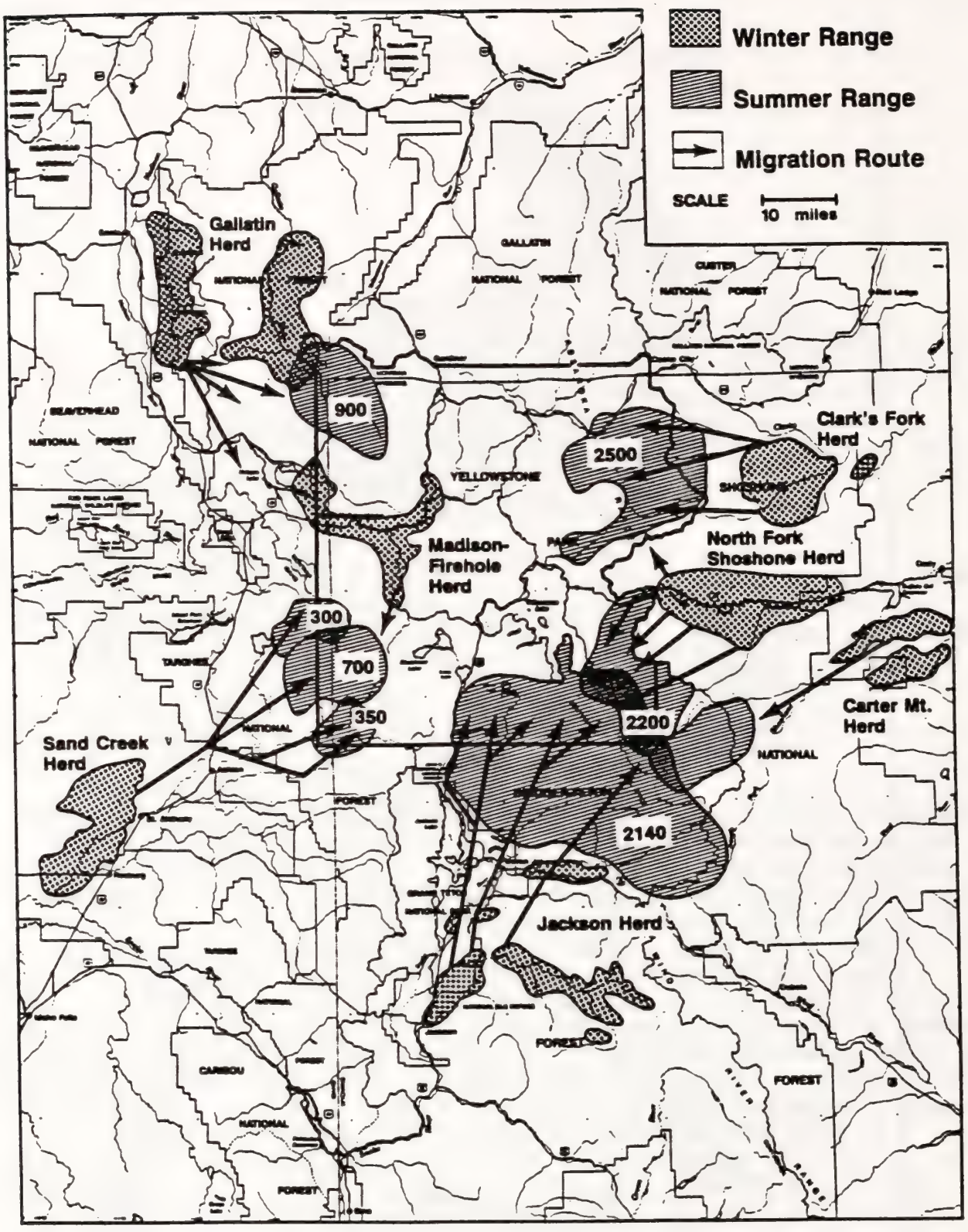


Fig. 2. Map showing the approximate winter ranges and summering areas for 7 elk herds other than the northern herd which uses Yellowstone National Park. Approximate numbers of summering elk within Yellowstone National Park are included.

RESULTS AND DISCUSSION

Ungulate Prey for Wolves

Typical average ungulate numbers on Yellowstone's northern winter range were about 18,500 (4.4×10^6 kg, Table 1) during the period 1980-1988 including average counts of 17,458 elk, 600 bison (Bison bison), 1,814 mule deer (Odocoileus hemionus), 392 pronghorns (Antilocapra americana), 273 bighorn sheep (Ovis canadensis), and an estimated 200 moose (Alces alces) (Houston 1982, Singer 1990, Meagher pers. comm., Fig. 3). Ratios of ungulates on Yellowstone's northern range averaged 100 elk:10 mule deer:3 bison: 2 pronghorn:1 bighorn sheep:1 moose. Ratios of biomass average) 100 kg elk: 6 kg mule deer:3 kg bison:1 kg moose:trace (tr) bighorn sheep:tr pronghorn.

Table 1. Average ungulate biomass ($kg \times 10^3$) on the winter and summer ranges of Yellowstone National Park for the period 1980-1988 (Houston 1982, Foss 1985, Chu et al. 1989, Hurley et al. 1989, Lockman et al. 1989, Singer 1990, Meagher pers. comm.). Biomass was calculated from live weights for Yellowstone National Park summarized in Houston (1982:157).

	Ungulate Biomass ($kg \times 10^3$)						
	Winter Ranges					Summer Ranges	
	Northern Range		Other				
Species	Within Park	North of Park and Less Available[1]	Park Winter Ranges	Total	(% Total)	Parkwide	(% Total)
Elk	3,532	400	428	4,360	(74)	7,013	(82)
Bison	238	0	1,031	1,269	(22)	1,288	(15)
Mule Deer	5	96	2	103	(2)	159+[2]	(2+)
Moose[3]	56	tr	28	84	(1)	84+	(1+)
Bighorn	12	5	---	~17	(tr)	19+	(tr)
Pronghorn	5	15	0	20	(tr)	27	(tr)
White-tailed deer							
Mountain Goat	<1	<3	0	<4	(tr)	<6	(tr)
Total	3,849	519	1,489	5,857	(100)	8,614	(100)

[1] Near the town of Gardiner, Montana, and outlying settlements where no sustained pack activity is predicted.
[2] Mule deer and moose are probably underestimated in summer.
[3] Population estimate from Houston (1982).

Ungulate numbers on three other winter ranges within Yellowstone Park (Gallatin (partial), Madison-Firehole, Thorofare Creek) totaled about 4,500 ungulates (1.8×10^6 kg, Table 1) during the 1980's (Figs. 1 and 3) including about 2,000 bison, 1,900 elk, >100 moose, and <30 mule deer (Singer 1990, Meagher pers. comm.). Ratios of ungulate numbers were 100 bison:95 elk:5 moose:1 mule deer for these areas. Ratios of biomass averaged 100 kg bison:42 kg elk:3 kg moose:tr mule deer.

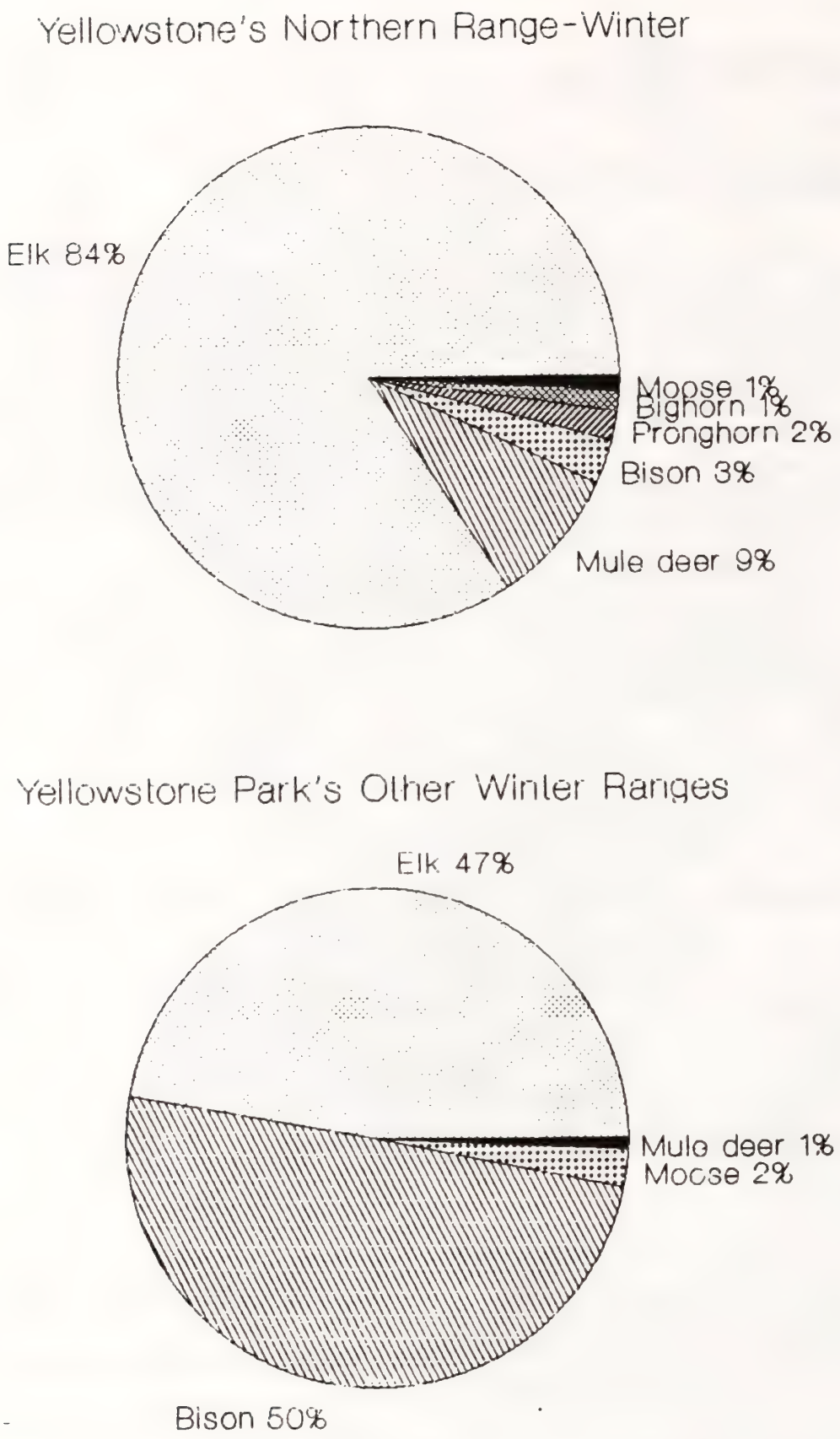


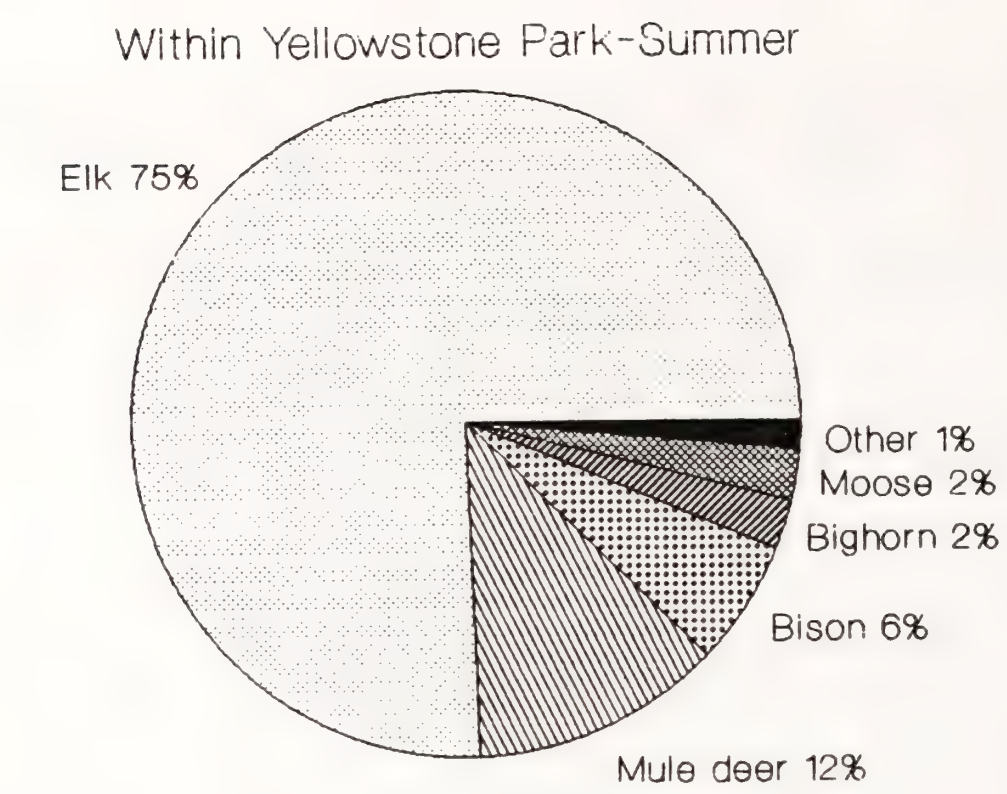
Fig. 3. Relative abundance of ungulates on Yellowstone's northern winter range (n = 18,555 ungulates) and other park winter ranges (n = 4,530 ungulates) (Madison-Firehole/Mary Mountain Thorofare, Pelican Gallatin) based upon average counts, 1980-1988.

Summer ungulate population estimates for Yellowstone Park exceeded 37,800 (Fig. 4), with a total ungulate biomass equaling 8.6 x 10 kg (Table 1) for the years 1980-1988. Portions of eight elk herds migrate into the park each summer, totaling approximately 31,000 elk from 1980 to 1988. Other ungulate population estimates for the same years were 2,500 bison, 100 white-tailed deer (Odocoileus virgianus), 100 mountain goats (Oreamnos americana), and 392 pronghorn. Approximate ungulate ratios in the park during summer were 100 elk:16+mule deer:8 bison:3+moose:3 bighorn sheep:1 pronghorn: < 1 white-tailed deer or mountain goat. Many more mule deer, bighorns and moose migrate into the park than previous counts indicated (Chu et al. 1989, Hurley et al. 1989, Lockman et al. 1989); therefore, their numbers are probably underestimated.

Chest heights and foot loading suggested elk, mule deer, bison, and pronghorns should be relatively easy prey for wolves in deep snow as would bighorn sheep when they occur away from escape terrain (Telfer and Kelsall 1984). Morphological indices, based upon foot loading and chest heights, rated the following species on their ability (from least to most difficulty) to move in snow: moose - 140, wolf - 135, elk - 118, bighorn sheep - 114, white-tailed deer - 112, bison - 95, and pronghorn - 81. In general, wolves have an advantage in pursuit of ungulates during late winter when crusts form and wolves are supported better than their prey (Formosov 1946, Nasimovitch 1955, Mech et al. 1971, Kolenosky 1972).

Where they occur together, wolves prefer mule deer over elk. Cowan (1947) reported that mule deer were killed 1.3 times more frequently than elk in Canada. White-tailed deer were preferred over elk during average winters, but elk were preferred during a severe winter in northwest Montana (D. Pletscher, pers. comm.). Wolves also prefer elk over bighorn sheep. In the Rocky Mountain national parks of Canada, bighorn sheep were killed only 0.17 times as often as elk, although they were 1.3 times more numerous (Cowan 1947). In another study, bighorn sheep provided only 3% of the year-round diet of wolves (Carbyn 1974a). Based upon relative availability, mule deer were killed 13 times more, elk were killed 0.28 times more, and bighorn sheep were killed 0.11 times more than the expected rate in winter (Carbyn 1974a).

Moose are killed less frequently than elk where the two species occur together. In Riding Mountain National Park, Manitoba, there was one moose for every 10.5 elk, but wolves killed only one moose for every 15 elk (Carbyn et al. 1987). Elk are nearly as large as moose, but wolves cornered elk in 1/6 the distance of moose, and, once cornered, elk were easier for wolves to kill (Carbyn et al. 1987).



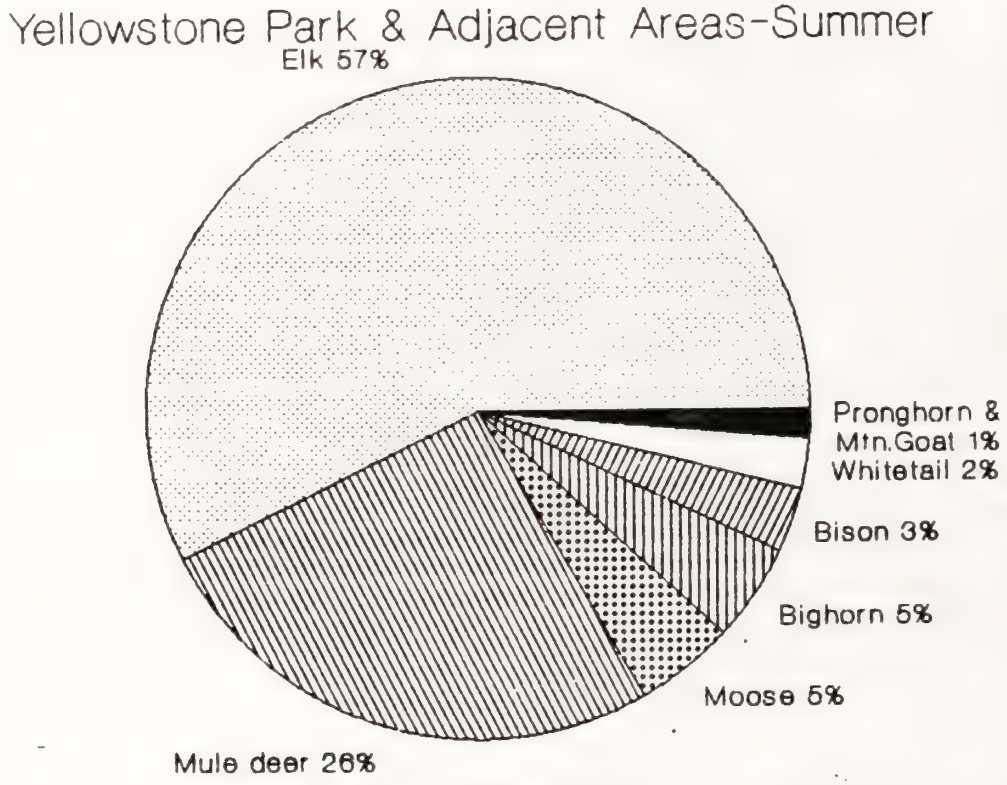


Fig. 4. Relative abundance, 1980-1988, for all ungulates (n = 37,804) that use Yellowstone Park during summer (n = 37,804) and for Yellowstone Park and adjacent areas (n = 82,057) based upon average population estimates. "Other" ungulates include pronghorns, bighorns, and mountain goats.

The majority of mule deer on the northern range winter immediately north of the park, where extensive human occupation will likely reduce wolf activity. A few wolves may use this portion of the northern range, but no sustained wolf pack activity is predicted since:

1) The population of Gardiner, Montana, is approximately 600, with another 300-400 residents living in the outlying areas between Yellowstone Park and Yankee Jim Canyon.

2) Hunting activity is intense in the area. Twenty-one full-time big game outfitters operate on the northern winter range along the Yellowstone River Canyon, and 18 outfitters operate in the adjacent Absaroka high country (D. Tyers, U.S. Forest Service, pers. comm.). The elk hunting season lasts about four months each fall and winter (about Oct. 19-Feb. 15), and about 10% of the Montana elk harvest occurs in the area.

3) Mule deer, which wolves would prefer, winter mostly in the valley floor near human habitation.

4) The area is mostly open big sagebrush (Artemesia tridentata) country and is less than one-half forested. Mule deer are widespread throughout Yellowstone Park during summer and will be widely available to wolves then.

The few white-tailed deer seen on Yellowstone's northern range are probably dispersers from nearby populations. Wolves will probably not reduce whitetails because no population winters within the park, and stable or expanding herds occur within 32 km of the park's boundaries. These areas will probably not support any significant wolf activity (e.g. Tom Miner Basin, Rock Creek, Fall River, upper Henrys Fork) due to proximity to human developments.

Pronghorn should be the most vulnerable park ungulate to wolves in snow (Telfer and Kelsall 1984), but Yellowstone's pronghorn winter on the outskirts of Gardiner, Montana, where snow depths are minimal, and wolves are predicted to avoid the area. Some pronghorn migrate into sagebrush-dominated higher valleys within the park each summer, and young fawns could be taken by wolves at this time.

Few observations of wolf predation are available from areas where bison and other ungulates occur together. Wolves are predicted to frequently pursue bison when bison are the most common, or the only ungulate species available. Wolves frequently pursued bison during the summer in Wood Buffalo National Park. Wolves approached, tested, or rushed bison in 79% of all wolf-bison encounters (Carbyn and Trottier 1987, 1988). Historically, healthy bison of all age classes were relatively safe from attack by wolves during the early years of Yellowstone (Meagher 1973). Bison should not be particularly vulnerable to wolves during winter on Yellowstone's northern range for the following reasons: 1) snows are shallower on the northern range than on the park's other two bison winter ranges (Meagher 1971, 1973); 2) elk, wolve's

preferred prey, greatly outnumber bison (100 elk:2 bison); 3) bison groups are scattered throughout the northern range; 4) bison fend off wolves as a group, and bulls are very aggressive towards wolves; and 5) bison calves are protected by their position in bison pods and calves can withstand prolonged attacks by wolves (Carbyn and Trottier 1987, 1988).

Bison will be killed by wolves in the Madison-Firehole/Mary Mountain area since bison are more abundant than elk (100 bison:95 elk) and in the Pelican Valley where only bison occur. Telfer and Kelsall's (1984) chest height and foot loading analysis suggests that bison would be vulnerable to wolves in deep snow. Oosenbrug and Carbyn (1983) reported that solitary bison are most vulnerable to wolves. They reported that a pack of wolves killed one bison every eight days in winter including a high proportion of adult males in Wood Buffalo National Park, Alberta. Van Camp (in prep.) reported that a large pack of wolves killed one bison every seven days in the Slave River lowlands, and 86% of these were cows or calves. Apparently wolves suppressed bison recruitment in the Slave River lowlands, although hunting, disease, and severe winters also contributed to the decline. In both studies, bison were the primary prey available. In conclusion, wolf effects on bison would likely range from relatively minor, on the northern range, to more significant on the Mary Mountain and Pelican Valley ranges.

Based upon prey numbers, spatial distributions, and vulnerabilities to wolves, the diet of wolves during winter on Yellowstone's northern range is predicted to be elk > bison > mule deer > moose > pronghorn > bighorn sheep. On Yellowstone's other three ungulate ranges, wolves are predicted to kill prey during winter in the order of most to least: elk ≅ bison > moose > mule deer. During summer in the entire park, wolves are predicted to kill prey in the order: elk > mule deer > bison > moose > bighorn sheep > pronghorn.

Wolf Packs and Territories

The opportunity apparently exists for 5-6 year-round wolf pack territories of approximately 90-150 km^2 on the northern range. About 2,000-4,000 elk winter only 6-16 km from summer ranges in the following areas: 1) Cache Calfee/ Mount Norris (NE), 2) Mirror Plateau (EC), 3) Buffalo Plateau-Telephone Basin (N), 4) Gardners Hole-Gallatin Mountains (NW), and 5) Cook-Folsom Peaks (NC) (Fig. 1). Perhaps another 2-3 packs could establish much larger territories of >750 km^2 that include portions of the northern range and elk summer ranges, 21-32 km from the northern range such as the following areas: 1) Pelican Valley (EC), 2) Upper Lamar (E), and 3) Hayden Valley-Bridge Bay (C) (Fig. 1). Single packs could establish year-round territories in the Madison-Firehole/Mary Mountain area (1,300-1,700 bison, 800-1,400 elk in winter) and possibly the Upper Yellowstone River-Thorofare area (100 moose, 500-700 elk in winter, Fig. 2), although the Thorofare area appears marginal for sustained winter wolf pack activity.

Four additional summer concentrations of elk occur in the park [Southwest (SW)- 1,400+ elk; Southeast (SE)- 2,200+ elk, South-central (SC)- 2,000+ elk; and the

Central Plateau (C)- 7,000-10,000 elk] (Fig. 1). Elk migrate 48-64 km from these areas to winter ranges (Brown 1985, Boyce 1989, D. Vales pers. comm., Smith and Robbins pers. comm.). Fewer than 100 ungulates winter in each of these locales suggesting the wolves would have to be partly or completely migratory. Wolves migrate 80-160 km between summer and winter caribou ranges in Alaska (Stephenson and James 1982), and as much as 360 km between caribou seasonal ranges in the Northwest Territories (Kuyt 1972). However, no instance of migratory wolves south of the arctic or boreal forest regions are reported.

In conclusion, 7-9 wolf packs with fixed territories could occupy Yellowstone's northern range; another 1-2 fixed packs could occupy the park's other winter ranges; and another 3-4 packs might be supported, but only if the latter were migratory or semimigratory (Total = 11-15 packs).

If each wolf pack plus loners averaged 10 wolves, this equates to 110-150 wolves for Yellowstone National Park. Biomass available would range from 57,426 to 78,309 kg per wolf during summer (110-150 wolves) and from 58,570 to 73,213 kg per wolf during winter (80-100 wolves). Winter densities of wolves are predicted to be 1 wolf/10-13 km^2 (70-90 wolves) on the northern range, and 1 wolf/40-80 km^2 (10-20 wolves) on the other park ranges. Summer densities of wolves parkwide would be 1 wolf/60-81 km^2 (110-150 wolves). If these scenarios hold true, winter densities of wolves on the northern range would be among the highest recorded (Mech 1970, Kuyt 1972, Van Ballenberghe et al. 1975), with biomass per wolf among the highest (Mech 1970, Keith 1983). Mech (1970) reported 1 wolf/26 km^2 appeared to be a maximum density, although concentrations of 1 wolf/10-15 km^2 have been observed (Kuyt 1972, Van Ballenberghe et al. 1975). Mech (1970:277) advanced the idea that when prey biomass exceeds 11,000 kg of prey per wolf, wolf predation cannot be considered a primary controlling influence on prey densities.

Theberge (pers. comm.) cautioned wolf:prey ratios be used in preliminary assessments only. Use of wolf:prey ratios are complicated by the following factors: 1) wolf consumption declines and wolf scavenging increases as prey declines, 2) wolf numbers lag in response to prey numbers, 3) wolf predation varies from compensatory to additive depending upon the proximity of the ungulate population to its nutrient-climate ceiling, and 4) the use of nonungulate prey and the speed of prey switching due to changing abundance or vulnerability of prey varies.

Ungulate Distributions after Wolf Recovery

Adult female ungulates with young calves may alter their habits more than other ungulate sex and age classes after wolf recovery. Cow moose with young calves frequent wolf-free islets within Isle Royale National Park and consume a poorer quality diet than cows without calves or yearlings (Edwards 1983). Moose cows with young calves frequent camps occupied by people, or human developed areas, apparently to avoid wolves on both Isle Royale (Stephens and Peterson 1984) and to avoid wolves and grizzly bears (Ursus arctos) on the Kenai Peninsula (E. Bangs pers. comm.) and in Denali National Park, Alaska, (J. Dalle-Molle

pers. comm.). Caribou (Rangifer caribou) cows with young calves demonstrate similar strong antipredator strategies (Bergerud 1980, Bergerud et al. 1984) including isolation of cows with calves on high slopes and consumption of poorer quality diets. Cows with calves skirt willow (Salix spp.) thickets, apparently to avoid ambushes by predators (Roby 1978) while bulls prefer the thickets for feeding. Newborn ungulates in Yellowstone Park are preyed upon by coyotes and grizzly bears (Robinson 1952, French and French 1990), so adult female ungulates may already exhibit antipredator behavior. Several ungulate antipredator strategies appear instinctive, such as hiding calves and fawns (elk and deer, Carbyn 1974a), traveling to separate calving areas (elk and caribou, Bergerud 1980), and winter yarding behavior -- grouping together for protection in addition to allowing access to beaten trails for quick escape from predators (whitetails, Messier and Barette 1985).

Adult ungulates may change their use of habitats slightly in response to wolves. Wolf researchers report little movement by groups of ungulates after wolves test or kill individuals (S. Fritts, L. Carbyn pers. comm.). Bighorn sheep stayed closer to steep, escape terrain in Jasper National Park after wolves reoccupied the area following a rabies control program (J. Stelfox pers. comm.). Ungulates occupying the fringes of winter concentrations are preyed upon more intensely by wolves (Fritts and Mech 1981, Nelson and Mech 1981, Messier and Barette 1985), and they may respond more to wolf presence. Hatter (1982) reported elk cow-calf groups on Vancouver Island increased summer range movements when wolf densities were high; elk preferred forest habitats, and black-tailed deer (Odocoileus hemionus peninsulae) bypassed spring ranges. Landscape features such as heavy timber downfall, cliffs, and open water may provide escape opportunities for elk and moose (Peterson and Allen 1974, Gunson 1986). Remnant populations of ungulates may respond more to wolves (Ferguson et al. 1988). Few studies, however, specifically addressed changes of habitat use by ungulates in response to wolves, so responses may have gone undetected.

Small populations of ungulates inhabit the thermal areas of Yellowstone National Park's interior during winter. In 1987-1989, one or two bull bison wintered at Little Firehole Meadows, and groups of 10-25 elk wintered at each of the following areas: West Thumb Geyser Basin, Shoshone Geyser Basin, Basin Creek, and Heart River Hot Springs. Near Old Faithful, 4-6 mule deer wintered, and, at Heart Lake Geyser Basin and the Bechler Meadows thermal areas, groups of 25-30 elk wintered. Both elk and bison are found in the Gibbon, Firehole, and Madison Rivers, and bison are found along Pelican Creek thermal areas (Craighead et al. 1973, Meagher 1973). Consequences of geothermal activity are shallower snows with greater access to forage. Forage grows all winter in warm meadows and along warm watercourses (Craighead et al. 1973). Deep snows surround all of the thermal areas of the park's interior.

Ungulates inhabiting the larger thermal areas of the park are predicted not to be particularly vulnerable to wolves during winter. Just as white-tailed deer escape from wolves in winter yards by running along any of the many crisscrossing beaten trails (Nelson and Mech 1981, Telfer and Kelsall 1984), park ungulates could escape from wolves on the relatively snow-free surfaces of the larger thermal areas.

Ungulates inhabiting the very smallest thermal areas during winter, consisting of only a few hectares or more could be reduced by wolves, since wolves could easily chase the ungulates into deep snows bordering the thermal areas. Population consequences would be insignificant since 4% of the elk and <10% of the park bison inhabit small thermal areas.

Wolf Effects on Ungulate Populations

The findings on wolf-prey relations from northern regions of North America should be applied with great caution to Yellowstone Park. Those studies were conducted over large contiguous areas where wolf immigration into wolf control zones was a significant factor (Gasaway et al. 1983, Ballard et al. 1987).

Wolf predation will likely result in slightly lower densities, younger age structure, and higher reproductive rates (compensatory reproduction) in unhunted park ungulate populations. Wolves killed mostly young of the year and older than prime-age adults in elk (Carbyn 1983), moose (Mech 1966, Pimlott et al. 1969, Peterson 1977), Dall sheep (Ovis dalli) (Murie 1944), white-tailed deer (Pimlott et al. 1969, Mech and Frenzel 1971), and caribou (Kuyt 1972). Compensatory reproduction could be substantial in the northern Yellowstone elk herd which is characterized by low calf:cow ratios in the absence of wolves (Houston 1982, Singer 1990). The timing and proximate cause of elk deaths will differ after wolf recovery. Winterkill of ungulates will probably decline.

Adult male:adult female ungulate ratios may vary after wolf recovery. Wolves killed more male adult ungulates than their occurrence in the white-tailed deer population (Pimlott 1967, Mech and Frenzel 1971), elk (Carbyn et al. 1987), caribou (Haber 1977; L. D. Mech, U.S. Fish and Wildl. Serv., pers. comm.), and bison (Oosenbrug and Carbyn 1983). But male:female ratios typically were higher in ungulate populations that were increasing, below habitat carrying capacity, or of low mean age. The influence of higher adult mortality rates on depressing male:female ratios were exacerbated in populations with an older average age. Male:female ratios might actually increase in unhunted park ungulates after they were subjected to wolf predation.

Wolf Effects on Other Predators

Coyote

Coyotes (Canis latrans) may be impacted by a wolf reintroduction. Few closely parallel examples exist, but coyotes probably will be less abundant in Yellowstone after wolf recovery since wolves frequently kill coyotes (Seton 1929, Young and Goldman 1944, Munro 1947, Stenlund 1955, Berg and Chesness 1978, Carbyn 1982). Coyotes were extirpated by wolves on Isle Royale (Mech 1966, Krefting 1969, Allen 1979). Coyotes expanded into several areas of North America after wolves disappeared (Silver and Silver 1969, Mech 1970) suggesting wolves suppressed coyotes. High densities of wolves in northeastern Minnesota

(1 wolf per 26 km^2) may have prevented coyote colonization of that region (Berg and Chesness 1978). In northeastern Alberta, coyotes tended to live primarily along wolf pack territory edges where the chance of encountering wolf packs was the lowest (Fuller and Keith 1980b).

Wolves and coyotes historically coexisted in Yellowstone National Park (Murie 1940) as they do in the Canadian Rocky Mountain national parks (Cowan 1947, Carbyn 1974b) and in Riding Mountain National Park (Carbyn 1982, Paquet 1989). Some competition between coyotes and wolves was reported from Riding Mountain National Park (Carbyn 1982). Coyotes avoided wolves more in mid to late winter when food was limiting than in early winter, and coyotes became rare after a period of relatively high wolf populations (Carbyn 1982). However, Paquet (1989) observed no spatial segregation between the two species. Coyotes did not avoid areas frequented by wolves, and although wolves occasionally killed coyotes, coyotes often trailed wolf packs at a safe distance. Wolves killed more elk than mule deer, but coyotes killed mostly deer and an occasional elk. Most coyote use of elk was scavenging of wolf kills. Paquet (1989) concluded that sympatric populations of wolves and coyotes existed where multiple species of ungulates occur and where the primary prey of wolves was larger ungulates such as moose, elk, or bison. Where deer are the key prey species for wolves, as is the case in Minnesota, the degree of dietary and ecological overlap increases. Less scavenging potential exists for coyotes, since wolves that kill deer leave few remains. Coyotes kill deer at all times of the year in Yellowstone National Park (Murie 1940:48, Robinson 1952), but Yellowstone National Park supports a multiungulate prey base, and elk, not deer, will be the key prey for wolves. Therefore, it is predicted that coyotes would not be extirpated in Yellowstone.

Red Fox

Red fox (Vulpes vulpes) are rare in Yellowstone National Park, but their numbers are predicted to increase following wolf recovery. Wolves occasionally kill foxes (Stenlund 1955, Mech 1966, Banfield 1974), and wolves typically chase foxes off carcasses, but foxes usually remain in the area until the wolves finish feeding (Magoun 1976). Peterson et al. (1982) reported that foxes usually are able to escape from wolves. Foxes largely benefit from wolves. During a period when snowshoe hares (Lepus americanus) were not abundant, the carrion from wolf-killed moose sustained red foxes on Isle Royale (Johnson 1970). Mech (1970) concluded that foxes mostly benefit from abandoned wolf kills, although he observed that both species robbed each other's food caches.

Any reduction in coyote numbers due to wolf recovery should benefit foxes. The presence of coyotes limited the habitat available to foxes in eastern Maine (Harrison et al. 1989). There, foxes were usually associated with riparian areas or lakeshores, but foxes did not use those habitats within coyote territories. Foxes established home ranges outside coyote territories or in boundary areas between coyote groups.

Wolverine

Wolverines (Gulo gulo) are killed by wolves, but Yellowstone National Park is so extensively forested (79%) that wolverines could escape from wolves by climbing trees. Three instances of wolves killing wolverines have been reported (Burkholder 1961, Boles 1976), but, in each case, tree escape was not possible. Murie (1963) observed three other attacks by wolves upon wolverines, and, in each case, the wolverines escaped by climbing trees. Wolves and wolverines coexist over large regions of northern Canada and Alaska, including treeless areas. However, little published information exists to conclude if competition could occur between the two species over the scavenging of carcasses.

Mountain Lion

Mountain lions (Felis concolor) and wolves would likely overlap to some extent in habitat use and food habits. Wolves killed two mountain lions in Glacier National Park, Montana (D. Pletscher pers. comm.). Little published information exists on population effects on either species.

Black Bear

Black bears (Ursus americanus) can become prey for wolves, although the heavily forested nature of Yellowstone National Park suggests black bears could escape to trees in most nondenning situations. Wolves have been observed to chase black bears (Rutter and Pimlott 1968), to tree black bears (Rogers and Mech 1981), and, in one instance, to kill a nondenning black bear (Young and Goldman 1944). Five instances were reported of wolves digging up, killing and consuming denning black bears (Rogers and Mech 1981, Horejsi et al. 1984, Paquet and Carbyn 1986). Cubs were present in two cases; in one instance, the cubs were killed; and, in the second instance, the cubs escaped by climbing a tree. The cubs of any bear species may be vulnerable in treeless areas. Wolves killed one of two polar bear (Ursus maritimus) cubs after separating one cub from the sow (Ramsay and Stirling 1984). Black bears might avoid treeless areas more in Yellowstone National Park after wolf reoccupation, but black bears may already avoid treeless areas due to the presence of grizzly bears.

Black bears have been observed to chase single wolves (Rogers and Mech 1981), and, in one case, a black bear killed an adult female wolf (Joslin 1966). Black bears usurp wolf kills (Mech 1970) as do grizzly bears (Murie 1981, Hornbeck and Horejsi 1986), but wolves may also usurp bear kills (Haber 1977, Ballard 1982).

A review of the possible effects of introduced wolves on Yellowstone grizzly bears suggested few effects on population numbers from wolf-bear interactions (Servheen and Knight 1990). Direct interactions, most of which were confrontations over food or young, appeared to favor neither species on the average (Servheen and Knight 1990). A few highly predatory/scavenging Yellowstone grizzly bears could be influenced by wolf reintroduction, but Servheen and Knight (1990) predicted any changes would be gradual with increasing wolf numbers, and bears would adapt.

Effects Upon Yellowstone Park Visitors

Viewing opportunities for ungulates are predicted to decline little, if at all, after wolf reintroduction. Elk populations may decline 15%-25%, and bison populations may decline 5%-15% after complete wolf recovery (Boyce 1990, Koth et al. 1990), thus reducing the total number of ungulates to observe. Few habitat or distribution changes are predicted except by adult female ungulates with young. Ungulates that frequent human developments should continue to be highly observable to visitors since these areas will be avoided by wolves (Stephens and Peterson 1984). Ungulate use of human developments may even increase after wolf reintroduction.

Wolves are typically shy animals that usually avoid humans where harvest by humans exists. Some wolves lose their fear of humans, such as where they frequent human garbage sources. Even after 40 years of total protection, Isle Royale wolves still exhibit a fear of man similar to that in a hunted population (Peterson and Morehead 1980). Yellowstone Park wolves are predicted to be similarly shy.

Humans may disrupt wolf activity, particularly near den sites. Fewer wolf kills of ungulates and four deserted wolf dens occurred in areas near human developments in Jasper National Park, Alberta (Carbyn 1974b). Wolves howled, left the area, and/or moved pups when disturbed at den sites (Haber 1968, Chapman 1979). However, low intensity disturbances seemed unlikely to cause significant pup mortality (Chapman 1979).

Management actions to protect wolves in U.S. national parks have varied considerably. Chapman (1979) recommended prohibiting human access within a 2.4-km radius of den sites and active rendezvous sites. He recommended closures lasting from four weeks prior to whelping until 1 August. To protect the location of den sites from visitors, Denali National Park staff closed eight areas averaging 42 km^2 (range 10-100 km^2) to protect wolf packs. These closures are irregularly shaped rather than concentric to prevent visitors from predicting the den locations (J. Dalle-Molle pers. comm.). In 1989, Denali National Park reduced the number of wolf closures from eight to four, but their size was increased to a mean of 100 km^2 (range 54-187 km^2) (T. J. Meier, Denali

Natl. Park, pers. comm.). The larger closure size in 1989 was used partially to coordinate with backcountry units and with bear closures. In 1990, only areas with active dens will be closed.

The smallest wolf closures are used in Voyageurs National Park where closures around active dens are circular and 0.8-1.6 km in radius. Voyageurs National Park managers restrict dogs and dogsled teams to the open ice areas of the park, attempt to increase public awareness of wolves, and work to increase prey abundance and diversity. Park managers are considering reintroducing caribou and possibly elk. Isle Royale National Park has been closed to winter use by visitors since 1975, largely to reduce disturbances to wolves and to reduce interference with long-term research (Peterson and Morehead 1980). Plans to build a new shoreline trail were dropped to protect wolves. The park is delineated into 46 travel zones, averaging 11.8 km^2. These zones are closed temporarily for active wolf dens, active wolf rendezvous sites, or other intense wolf activity. The zones are reopened as soon as wolves leave the area. Visitor activities in Glacier National Park, Montana, have been affected little by wolf activity. Two road sections have been closed for a few weeks during the beginning of the visitation period, but the sections were opened as soon as wolves moved pups from den sites (W. Brewster pers. comm.). It may be necessary to close a few small areas in Yellowstone Park during denning by wolves. Some wolf denning should take place in existing bear management areas or remote areas where no further action would be necessary. Most closures near wolf dens in the U.S. national parks last from denning, about 1 April, until the pups are moved, usually about mid-June.

Unanswered Questions

Insufficient information was available to answer a number of questions concerning the proposed wolf recovery into Yellowstone Park including:

1. Will some wolf packs be migratory? How will packs exploit the large summer elk concentrations in the park's interior?

2. How efficient will wolves be at taking bison? While two studies from Canada suggest wolves may take bison frequently where only bison are available, there is no information on kill rates of bison from multiungulate ecosystems such as Yellowstone.

3. How much will wolves use the northern range north of the park boundary where human activity is high?

4. Will wolves take moose on the northern range and cause a moose decline? Alternatively, will moose in the area be invulnerable to wolves and be infrequently taken as prey?

5. Will predation by wolves on the largely unhunted park elk and bison herds result in an increase in reproductive rates or in an increase in survival rates of ungulates? Will ratios of adult males in ungulate herds increase or decline after wolf reoccupation?

These questions can only be answered if wolves are actually reintroduced into the Yellowstone ecosystem.

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POSSIBLE EFFECTS OF A RESTORED WOLF POPULATION ON GRIZZLY BEARS IN THE YELLOWSTONE AREA

Christopher W. Servheen
U.S. Fish and Wildlife Service
University of Montana
Missoula, MT 59717

Richard R. Knight
Interagency Grizzly Bear Study Team
Forestry Sciences Laboratory
MSU Campus
Bozeman, MT 59717

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Christopher W. Servheen, U.S. Fish and Wildlife Service, NS 312, University of Montana, Missoula, MT 59812

Richard R. Knight, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, MSU Campus, Bozeman, MT 59717

EXECUTIVE SUMMARY

Brown bears (Ursus arctos) and gray wolves (Canis lupus) coexist throughout much of North America and Eurasia. A review of available literature on wolves and brown bears from the limitation of brown bear numbers by wolves or reports of limitation of wolf numbers by brown bears. Letters were sent to numerous scientists in the Soviet Union and Europe to solicit any opinions or unpublished information of wolf-brown bear interactions. None of those who responded indicated that wolves could pose a significant threat to brown bear populations. Reports of observed wolf-grizzly bear interactions from Alaska were summarized and did not indicate any significant detriment to either species due to interactions. In general, information indicates that the two species will interact over food sources but at few other occasions. Most interactions are characterized by mutual avoidance. Few instances of direct mortality to either species as a result of interactions are available.

In the Yellowstone area, wolves will change the numbers and distribution of ungulates that are used by grizzly bears as food. The significance of this change is speculative at this time. It is likely that any change to the ungulate population as a result of wolves would be gradual and grizzly bears would successfully adapt to this change over time. This change in ungulate numbers and distribution would be the most important impact of an increasing wolf population to grizzly bears in the Yellowstone area. It seems reasonable to assume that grizzly bears would adapt to these changes with little detrimental affect to grizzly numbers or survival.

POSSIBLE EFFECTS OF A RESTORED WOLF POPULATION ON GRIZZLY BEARS IN THE YELLOWSTONE AREA

Christopher W. Servheen, U.S. Fish and Wildlife Service, NS 312, University of Montana, Missoula, MT 59812

Richard R. Knight, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, MSU Campus, Bozeman, MT 59717

ABSTRACT: A review of the literature and contact with scientists in other countries revealed little evidence that sympatric gray wolf (Canis lupus) and grizzly bear (Ursus arctos horribilis) populations have any significant demographic effect on each other. There are references of mortalities to both species because of interactions, but these instances are rare. No evidence was found of impact on survival or successful reproduction to populations of either species due to interspecific interactions. Interactions are apparently mediated by the age and sex of participants, and also by the location, reason for interaction, and behavioral experience of the animals involved. No patterns emerged regarding the outcome of interactions.

Predator control eliminated the gray wolf (Canis lupus) from Yellowstone National Park by the 1920's (Murie 1940:16). Weaver (1978) reported two sightings in the 1930's. Cole (1969) stated that mission-oriented research in the National Park Service involves development of management procedures to compensate for departures caused by human actions. There is increasing impetus both within the scientific community and the public to reintroduce the wolf to Yellowstone Park to restore some measure of ecological completeness.

The gray wolf is a highly-efficient predator that some laypersons fear could seriously deplete other animal populations. Since 1975, millions of dollars have been spent on grizzly bear research and management directed toward recovery from threatened status. This report examines possible interactions between introduced gray wolves and Yellowstone grizzly bears (Ursus arctos horribilis) to predict the effects of gray wolf population restoration on the existing grizzly bear population.

METHODS

Scientific and popular literature from North America, in addition to scientific literature from Europe, was reviewed for published records concerning interactions between gray wolves and bears. Twenty-three scientists and wildlife managers in the Soviet Union were contacted by letter to assess the existence of records of gray wolf-brown bear (Ursus arctos) interactions in the Soviet Union. Of the 23 contacted, eight detailed responses were received. (For a copy of these responses contact: Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190.)

HISTORICAL PERSPECTIVE

Gray wolves and grizzly bears coexisted for centuries in and around the Yellowstone area. Gray wolf and grizzly bear remains have been found in deposits in Lamar Cave; the gray wolf bones were below a level that was carbon dated at 960 years before present (Hadly 1989). There are no recorded incidents of interaction between gray wolves and grizzly bears in the Yellowstone area. Relative numbers of both species prior to human encroachment are difficult to determine.

Prior to the establishment of Yellowstone Park and during its early years, all predators were controlled by whatever means available. During the 1870's and through the mid-1880's, intense market hunting of wild game existed inside and outside of the park (Houston 1982:11). This market hunting likely lowered densities of prey species for resident gray wolves. The Superintendent's Report for 1877 stated that "many carcasses were strychnine-poisoned for wolf, coyote and wolverine in 1874-75." Haines (1977:80) states, "coyotes, wolves, cougars, wolverines, and bears were shot on sight by employees and visitors, prior to the era of army management."

By 1914, after a quarter of a century of U.S. Army protection of large game animals, wolves had increased noticeably in northern Yellowstone Park. Concerted efforts to exterminate them resulted in a minimum of 136 wolves killed in dens, trapped, shot, and poisoned within the park from 1914-1926 (Weaver 1978:9).

The original equilibrium between wolves and grizzly bears is difficult to assess. Wolves may have been present in greater numbers than were evident and simply not seen. Mech (1970:9) states, "Anyone who has spent much time in wolf country will verify that the wolf is one of the wildest and shyest animals in the northern wilderness. Many an experienced woodsman has lived a lifetime without even glimpsing a wolf in its natural surroundings." Early efforts at extermination may have had a far greater effect on wolves than on bears. Most of the efforts directed at killing wolves either to protect furbearer trap lines and later for gray wolf hides took place through strychnine-poisoning in the winter when bears were hibernating. Gray wolves were also persecuted in areas surrounding the park; bounties were paid on 80,730 dead wolves in Montana between 1883 and 1919 (Lopez 1978:183). Government agents removed 413 Montana wolves from 1918-1930, the last one in 1945. In Wyoming and South Dakota, 508 wolves were killed between 1918 and 1923, the last one in 1940 (Weaver 1978:20).

KNOWN INTERACTIONS

Gray wolves and grizzly bears still coexist over vast areas of Canada, Alaska, and Eurasia. Some insight into probable interactions between the two species in Yellowstone can be gained from published observations.

Pulliainen (1965) stated that wolves and bears do not often occupy the same regions in Eurasia, and that bears in Finland decreased as wolves increased. However, his distribution maps for Finland did not support this contention. Fedosenko (pers. comm.) believes that Pulliainen was mistaken since the two species do coexist throughout much of the Soviet Union. Mech (1970:283) believes that declines in bear populations where wolves are also present could be explained by other factors.

In the Soviet Union, Lavov (pers. comm.) notes an inverse relationship between high gray wolf numbers and high brown bear numbers in Byelorussia, U.S.S.R. However, he discounts the impact of either species on the direct mortality of the other species in the Berezina Reserve. Lavov has only seen one three-year-old brown bear killed by wolves from 1950-1970 and "a few" instances of bear fur in scat of gray wolves.

Kaal (pers. comm.) states that gray wolves and brown bears cohabit basically the same biotype in Estonia, U.S.S.R., with a minimum of problems. Schevchenko (pers. comm.) has conducted field investigations in the Carpathian Mountains in the western Soviet Union along the Romanian border for 20 years without noting any negative interactions between gray wolves and brown bears.

Frkovic et al. (1987a,b) have compiled 40 years of mortality records for gray wolves and brown bears in Yugoslavia where both species coexist in significant numbers. Although they do report an unknown category for cause of death, they mention no mortalities attributable to interspecific interaction.

Eugene (pers. comm.) notes that "there are no sharp antagonistic or competitive relationship(s) between gray wolves and brown bears in the Soviet Far East, but there is no competition because of high general biomass of prey objects. There are more than 250 wild ungulates per one wolf on the South of the region." In Yellowstone National Park, with 100 wolves, the wolf-ungulate ratio would be roughly 1:225 in winter and 1:378 in summer (Singer 1990a).

Van Ballenberghe (1987) cites Haber (1987) as reporting wolf:moose (Alces alces) ratios of 1:17-26 in the Savage wolf pack territory in Denali National Park from 1970-1973. Fall moose calf:cow ratios were high in spite of the low moose:wolf ratios. When the Savage pack declined to two or three wolves, moose calf survival remained relatively low. Brown bear predation may have been responsible for persistently low recruitment of moose calves to adults 1974-1982. In 1973, the bear:moose ratio in Denali National Park was 1:8. Here, then, is a case where low ratios of prey to both wolves and bears would seem to produce maximum competition, even potential population depression of one or the other species, yet that has not been observed.

Haber (1987), reporting on wolf-bear tradeoffs in Denali National Park, concluded that "(brown/grizzly) bear numbers, distribution, and seasonal shifts have changed little since 1966." Haber cited other longtime observers at Denali National Park who felt there had been little change in bear numbers since at least the 1920's and 1930's.

To our knowledge, there are no documented cases where gray wolves and brown bears have negatively influenced each other on a population basis in either Canada or Alaska.

DIRECT INTERACTIONS

Murie (1944) has summarized gray wolf-grizzly bear relationships in Mount McKinley (Denali) National Park as follows:

> As a rule grizzlies and (gray) wolves occupy the same range without taking much notice of each other, but not infrequently the grizzlies discover wolf kills and unhesitatingly dispossess the wolf and assume ownership. This loss is usually not a serious matter to the wolves, for if food is scarce, wolves will generally consume kills before bears find them. In the relationship existing between the two species, the wolves are the losers and the meat-hungry bears are the gainers.

Murie (1944) describes several skirmishes where no damage was sustained by either species.

Ballard (1982:77) summarized his observations on wolf-bear interactions in the Nelchina Basin, Alaska, as follows:

> My observations indicated that (gray) wolves do occasionally kill bears. The result of gray wolf-brown bear encounters, therefore, may be an additional source of natural mortality not previously documented for either predator species. Whether it is a significant source of mortality for either species remains unknown.

From 1966-1974, Haber (1987) recorded 36 wolf-bear interactions within wolf pack territories in Denali National Park. Of the 36 interactions, 19 took place at ungulate carcasses. Wolves won nine of the 19. Of the 36 interactions, 17 were not at carcasses. In those cases, wolves harassed the bears or tried to take cubs, and the bears retreated.

Lent (1964) observed a gray wolf and a grizzly bear sharing the same carcass. Hornbeck and Horejsi (1986) documented a four-year-old female grizzly bear displacing three or four wolves from a moose kill. Even though the wolves were active and howling within 300 m of the bear, she was reluctant to leave the kill.

Paquet and Carbyn (1986) recorded three instances of wolves digging up and killing cubs of hibernating American black bears (Ursus americanus) in Riding Mountain National Park, Manitoba, but believed that it was not a common phenomenon, since over 2,000 wolf scats collected in this area did not contain

any evidence of bear remains. Pimlott et al. (1969:63) recorded one instance of a black bear killing an adult wolf in Algonquin Provincial Park, Canada, but believed that there was probably little competition between the two species.

Steven Fritts (U.S. Fish and Wildl. Serv.) has collected 70 unpublished wolf-bear incidents and has consented to let us summarize them (Table 1). The results (Table 1) show no discernible trend of negative results to wolves or grizzly bears because of these interactions. The result of each interaction may be mediated by complex factors including age, sex, and reproductive status of both species, prey availability, hunger and aggressiveness of both species, numbers of animals, and previous experience in interacting with the other species, or any combination of these.

On the average, direct interaction between wolves and grizzly bears appears to be a standoff. Given the high degree of individuality in both species; this is not surprising. All serious confrontations appear to be in defense of food or young. There is no evidence that the occasional direct confrontation has any population effect on either species.

INDIRECT INTERACTIONS

The most significant indirect interaction between gray wolves and grizzly bears is probably in competition for food. While gray wolves must kill prey and depend entirely on meat, grizzly bears can subsist on vegetation and take meat opportunistically. Elk (Cervus elaphus canadensis) would be the most abundant prey species for gray wolves in Yellowstone Park (Singer 1990a). Elk are a significant portion of the diet of the Yellowstone grizzly bear (Mattson et al. 1990). Grizzly bears consume large amounts of elk in early spring both as carrion and by preying upon winter-weakened individuals. Grizzly bears are also efficient predators on newborn elk calves and commonly prey on adult bull elk during and after the rut. A few grizzly bears have learned to kill adult elk during the summer months. Depending on the size of the prey resource and the numbers of both predators, some competition related to elk is possible.

The most severe competition would likely be in spring after bears come out of the den. Competition during spring would be from direct competition for available carrion and winter-weakened animals, as well as due to possible reduction in elk numbers because of gray wolf predation. Grizzly bears use approximately 34% of the available carrion distant from open roads within Yellowstone Park on the northern range (Green 1989) and 30%-100% of available carrion distant from open roads and recreation site developments in the Firehole-Gibbon area of the park (Henry and Mattson 1988, Green 1989). Grizzly bears compete with other scavengers for elk carcasses in both areas, and the addition of wolves might intensify this competition or be merely compensatory with the other scavengers. In the Firehole-Gibbon area, grizzly bears use bison (Bison bison) carcasses three times as intensively as elk carcasses, and there is no competition because other scavengers are apparently unable to open bison carcasses. We assume gray wolves could open bison carcasses and thus would compete directly with grizzly bears for winter-killed bison carrion.

Table 1. Summary of unpublished wolf-grizzly bear interactions (data courtesy of S. Fritts, U.S. Fish and Wildlife Service, pers. comm.).

	Interaction Type															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
Number of occurrences	7	2	2	1	3	15	2	5	9	4	5	8	3	2	2	70
Outcome																
Bear wins	2	--	1	1	--	3	--	--	--	--	--	8	3	--	1	19
Wolf wins	--	1	--	--	3	6	--	5	1	--	5	--	--	2	--	23
Neither win	5	1	--	--	--	3	1	--	8	--	--	--	--	--	--	18
Both win	--	--	1	--	--	--	--	--	--	--	--	--	--	--	1	2
?	--	--	--	--	--	3	1	--	--	4	--	--	--	--	--	8
Numbers																
B>W	2	--	--	1	--	5	2	--	2	4	--	2	--	--	1	--
W>B	3	1	--	--	3	5	--	3	6	--	5	3	3	1	1	--
B=W	2	1	2	--	--	5	--	2	1	--	--	3	--	1	--	--
Site																
Feeding	7	2	2	1	3	2	--	5	3	--	5	8	3	2	1	44
Wolf den	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	4
Rendezvous	--	--	--	--	--	2	--	--	1	--	--	--	--	--	--	3
Other	--	--	--	--	--	7	2	--	5	4	--	--	--	--	1	19
Female with cubs																
No. occurrences	2	--	--	--	--	5	2	--	1	3	--	2	--	--	1	16
Outcome																
Bear wins	2	--	--	--	--	3	--	--	--	--	--	2	--	--	1	8
Wolf wins	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1
Neither wins	--	--	--	--	--	1	1	--	1	--	--	--	--	--	--	3
?	--	--	--	--	--	--	1	--	--	3	--	--	--	--	--	4

Bear/Wolf Interaction Types

1) Bear feeding, wolf in area, no bear reaction.
2) Wolf feeding, bear in area, no wolf reaction.
3) Bear and wolf feeding on same kill at same time.
4) Bear feeding on wolf kill, wolf not present.
5) Wolf feeding on bear kill, bear not present.
6) Bear/wolf fight/chase.
7) Wolf stalking bear.
8) Wolf feeding on bear.
9) Wolf and bear in same area.
10) Other, information not specific.
11) Wolf displaces bear from kill.
12) Bear defends kill from wolf.
13) Bear displaces wolf from kill.
14) Wolf defends kill from bear.
15) Bear kills animal wounded by wolf.

Total numbers of gray wolves the Yellowstone area could support, their distribution, and their effects on the prey base are highly conjectural at this point. Singer (1990b) considers the number of ungulates present within Yellowstone National Park adequate to sustain a minimally-recovered population of 100 gray wolves, even considering the multipredator complex in the ecosystem. Boyce (1990) estimates that average elk numbers may be reduced by 15%-25% if gray wolf recovery is accomplished. Garton et al. (1990) modeled the potential effect of a restored gray wolf population on the northern elk herd in the park. They projected that nine packs totaling approximately 75 gray wolves would decrease the northern elk population by 10% or less. Fifteen North American wolf-ungulate experts (Koth et al. 1990) expected that, 10 years after gray wolf reintroduction, assuming a population of 10 packs of 10 wolves each, wolves would reduce elk and bison populations parkwide by less than 20%.

We are uncertain about the importance of spring carrion to the grizzly bear population. Yellowstone is unique among North American grizzly bear habitats in the large amount of spring carrion and winter-weakened ungulates available annually. Most grizzly bear populations do well without this abundance of carrion now available in Yellowstone. On the other hand, Yellowstone does not have the abundance of alternative spring foods present in other areas; the Madison-Firehole is impoverished in noncarrion spring foods. The high-quality nutrition provided by carrion may also help compensate for a lack of midsummer fruit crops in Yellowstone. Bears in northern Yellowstone may benefit from usurping wolf kills. It is unknown whether the availability of gray wolf ungulate kills would compensate for reduced winter-killed carrion as a result of potential wolf reduction of ungulate numbers.

There remains a question of the effect of gray wolves restored into an ecological system from which they have been absent for 50-80 years. Filonov (1980) analyzed 25-30 years of data from nine RSFSR nature reserves. When wolves were greatly reduced or eliminated, disease and starvation substituted for wolf predation. Filonov (1980) found that "in Darvinsky Reserve, as a result of the great reduction in wolves, moose losses from wolf predation were reduced by 14 times, but at the same time, bear predation increased three-fold and mortality caused by diseases by more than 10 times. When wolf numbers increased, moose losses from predation decreased 1.5 times and mortality from diseases ceased." Filonov concluded: "Even local extirpation of predators such as the wolf does not change the level of natural mortality rate much, but it does influence population structure and the physical condition of the prey. Therefore, extirpation of large predators in nature reserves is not beneficial." Fifteen North American wolf-ungulate experts agree that changes in behavior and distribution of ungulates as a result of wolf restoration will be minor (Koth et al. 1990). To the extent that this change affects over-winter mortality and subsequent carrion availability, it may have some effect on the grizzly bear population.

Several correspondents from the Soviet Union note the limited effect of wolves on brown bears because bears are omnivorous and can use other foods if wolves change the availability of protein sources. Some grizzly bears in the Yellowstone area may be more dependent on ungulates than are many brown bear

populations in the Soviet Union. The restoration of gray wolves to the Yellowstone area could have the greatest effect on these grizzly bears dependent on ungulates. However, Haber (1988) reports large bear populations throughout northeastern British Columbia and that bears prey heavily on ungulates where wolves are present. Singer (1987) documented that, during 1984 and 1985 in Denali National Park, grizzly bears killed 22 collared caribou (Rangifer caribou) calves while wolves killed only eight calves, demonstrating that predatory grizzly bears compete with wolves very successfully for newborn calves. Since the slight changes anticipated in ungulate distribution and availability to bears will be gradual with increasing gray wolf numbers, it is reasonable to assume that grizzly bears could adapt to those changes.

In summary, available information suggests little, if any, effect on population numbers from gray wolf-grizzly bear interactions. Some initial change in bear-ungulate relations is expected, but this change would be gradual and grizzly bears are likely to adapt successfully to it.

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EFFECTS OF RESTORING WOLVES ON YELLOWSTONE AREA BIG GAME AND GRIZZLY BEARS: OPINIONS OF FIFTEEN NORTH AMERICAN EXPERTS

University of Minnesota
Cooperative Park Studies Unit
Department of Forest Resources

Barbara Koth, Assistant Extension Specialist
Department of Agricultural and Applied Economics

David W. Lime, Adjunct Professor and Research Associate
Department of Forest Resources

Jonathan Vlaming, Research Assistant
Department of Forest Resources

EFFECTS OF RESTORING WOLVES ON YELLOWSTONE AREA BIG GAME AND GRIZZLY BEARS: Opinions of Fifteen North American Experts

Barbara Koth, David W. Lime, Jonathan Vlaming, Cooperative Park Studies Unit, University of Minnesota, Department of Forest Resources, 110 Green Hall, St. Paul, MN 55108

EXECUTIVE SUMMARY

The opinions of 15 North American gray wolf (Canis lupus) and wolf-prey researchers known for their studies of the interrelations among wolves, grizzly bears (Ursus arctos) and prey species were examined. Panelists addressed questions relating to the potential effects of a reintroduction of wolves to Yellowstone National Park on 1) wolf prey in the park, 2) the population of Yellowstone grizzly bears, and 3) big game hunting in areas surrounding the park.

A modified Delphi technique was used to conduct the study. This approach called for questions to be answered by experts followed by a collation of responses by project coordinators. Subsequent follow-up questionnaires were sent to the experts for further inquiry. Between late September and late December 1989, panelists were contacted three times and asked both general and specific questions about the issues. With each successive contact, their opinions were compiled, and new or more probing questions were addressed. The end product represented the panelists' best judgments on a variety of concerns and topics regarding the reintroduction of wolves to Yellowstone National Park. The following are the most salient results of their deliberations.

Major Findings:

1) Panelists unanimously agreed that wolves were part of the original Yellowstone National Park ecosystem.

2) The core wolf population should be centered in Yellowstone National Park, but the application of artificial or political boundaries might not sustain recovery levels.

3) A viable wolf population of about a dozen wolf packs that spend the majority of their time within Yellowstone National Park seemed realistic after the population has stabilized (within 20 years after reintroduction).

4) If wolves are reintroduced, extinction of any prey species, elk (Cervus elaphus), mule deer (Odocoileus hemionus), moose (Alces

alces), bison (Bison bison), pronghorn (Antilocapra americana), bighorn sheep (Ovis canadensis), and mountain goats (Oreamnos americana) was thought to be extremely unlikely.

5) There should be relatively minor changes in prey species' behavior and distribution if wolves were reintroduced to Yellowstone National Park.

6) Elk and mule deer should be the primary prey for wolves -- elk throughout the year, mule deer in summer. Other prey species should be relatively minor food sources.

7) Panelists unanimously agreed that wolves and grizzly bears can coexist. However, there were differing opinions about specific impacts of wolf reintroduction on grizzly bears, particularly whether wolf predation should provide grizzly bears with more protein from wolf-killed carcasses and a more consistent carrion supply. All panelists did call the overall impact on grizzly bears "slight" or "neutral."

8) Reduced big game hunting levels should not be an automatic requirement if wolves were restored to the greater Yellowstone ecosystem. Reduced hunting levels should be implemented only when necessary and then only in conjunction with wolf control measures and other prey population management tools.

9) More research is needed to better understand the interrelations among wolves, grizzly bears, prey species, and big game hunting in areas surrounding the park.

More specific findings addressed the following issues:

1) wolf numbers, 2) wolf movements, 3) general impacts of wolves on prey species, 4) specific impacts of wolves on large ungulates -- elk, mule deer, moose, bison, pronghorn, bighorn sheep, and mountain goats, 5) impacts of wolves on grizzly bears, and 6) effects of reintroduced wolves on big game hunting in areas outside Yellowstone National Park.

Wolf Numbers:

1) Panelists estimated a mean of 13 wolf packs would spend the majority of their time in Yellowstone National Park after the wolf population was established.

2) To most panelists, a large number of packs (over 25) seemed unlikely.

3) Panelists estimated a mean pack size of seven to ten individuals.

4) Panelists estimated an average total in-park wolf population of 150 individuals would spend the majority of their time in Yellowstone National Park.

5) Panelists estimated five to ten additional packs would attempt to establish territories located primarily outside Yellowstone National Park.

Wolf Movements:

1) Wolves have the potential to locate nearly anywhere in Yellowstone National Park, but the most likely area of wolf colonization would be in the north-central region; some areas would be lightly occupied, if at all.

2) A stable territorial mosaic of wolf packs should develop within 20 years after reintroduction. Territories should change in response to changing prey distributions, prey abundance, and pack size and dominance.

3) In summer, most wolves should be within park boundaries and wolf activity should concentrate around den sites and should take advantage of calving by mule deer, elk, bison, and moose within Yellowstone National Park.

4) In winter, wolf packs should hunt mainly in areas of low elevation where ungulates, particularly elk, aggregate.

5) A consensus could not be reached concerning when packs might leave the winter range, how often packs would visit major prey areas within their territories in winter, and whether winter hunting would commonly occur as a pack or periodically as a subunit of the pack.

General Impacts of Wolves on Ungulates:

1) Ungulate species, in the order of most to least vulnerable, were as follows: elk, mule deer, moose, bison, pronghorn, bighorn sheep, and mountain goats.

2) Elk were expected to be the primary prey species for wolves in all seasons. Secondary prey would be mule deer, moose, and bison.

3) Most distribution changes of prey populations should be relatively local changes in animal movements, implying little geographical and behavioral distribution impacts.

Impacts of Wolves on Elk:

1) Elk were expected to be the primary prey for wolves in all seasons.

2) There should be moderate or little change in elk behavior and distribution if wolves were reintroduced to Yellowstone National Park.

3) Wolf predation should induce an initial decline in elk numbers that should reduce nutritional stress and improve reproduction.

4) Ten years after wolf reintroduction, assuming a wolf population of ten packs of ten wolves each, a reduction in the elk population of less than 20% was expected.

Impacts of Wolves on Mule Deer:

1) Mule deer might be a primary prey for wolves during the summer and a secondary prey for the rest of the year.

2) There should be moderate or little change in mule deer behavior and distribution if wolves were reintroduced to Yellowstone National Park.

3) Ten years after wolf reintroduction, assuming a stable wolf population of ten wolf packs of ten wolves each, a reduction in the mule deer population of between 20% and 30% was expected.

Impacts of Wolves on Moose:

1) Moose were considered potential prey for wolves, although panelists felt there was not enough information to formulate an opinion on whether moose would provide an important prey base for wolves.

2) There should be moderate or little change in moose behavior and distribution if wolves were reintroduced to Yellowstone National Park.

3) Ten years after wolf reintroduction, assuming a stable wolf population of ten wolf packs of ten wolves each, a reduction in the moose population of between 10% and 15% was expected.

Impacts of Wolves on Bison:

1) Panelists held widely varying opinions about the level of utilization of bison as wolf prey. Wolves might prey on bison only occasionally, but bison also had the potential to be major prey depending upon a variety of factors such as type of wolf reintroduction and hunting skills developed over time.

2) There should be little or no change in bison behavior and distribution if wolves were reintroduced to Yellowstone National Park.

3) Ten years after wolf reintroduction, assuming a stable wolf population of ten wolf packs of ten wolves each, a reduction in the bison population of less than 20% was expected.

Impacts of Wolves on Pronghorn, Bighorn Sheep, and Mountain Goats:

1) Pronghorn, bighorn sheep, and mountain goats would be available prey for wolves but would not likely be an important food source for them.

Impacts on Grizzly Bears:

1) Wolves would provide some carrion for grizzly bears, and some occasional wolf-bear conflicts might arise during competition for carcasses. Direct interspecies killing should be insignificant.

2) Grizzly bear distribution and behavior were not expected to change if wolves were reintroduced to Yellowstone National Park.

3) The omnivorous food habits of grizzly bears mean that grizzly bear densities are not strongly linked to ungulate densities.

Impacts of Wolves on Big Game Hunting in Areas Surrounding the Park:

1) Panelists were evenly split over whether reduced hunting levels would be a necessary concession that comes with wolf restoration.

2) Elk harvest levels might be reduced after wolf restoration, but, at present, elk are generally hunted below maximum sustained yield. No consensus was reached regarding mule deer, bison, and moose hunting. Projections indicated that harvest levels for pronghorn, bighorn sheep, and mountain goats would not need to be reduced.

3) According to the majority of panelists, sport hunting for any prey species should not have to be eliminated, even at higher pack levels (25 packs or more).

4) All panelists agreed that it cannot be assumed that a reduction in hunting would simply make up for wolf kills in an additive manner, because sport hunting and predation target different animals.

5) Hunting and wolf population control must be discussed as integrated factors. The objective outside Yellowstone National Park should be wolf population control, not eradication.

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EFFECTS OF RESTORING WOLVES ON YELLOWSTONE AREA BIG GAME AND GRIZZLY BEARS: OPINIONS OF FIFTEEN NORTH AMERICAN EXPERTS

A group of scientists convened to synthesize their opinions and best judgments on the reintroduction of the gray wolf (Canis lupus) to Yellowstone National Park. The group was primarily comprised of experts who have studied the interactions among wolves, grizzly bears (Ursus arctos) and prey species; and included experts in system modelling, the historical view of wolf research, and on-site experience. Specifically, the group focused their assessment on the potential effects of a reintroduced population of wolves on: 1) their potential prey in Yellowstone National Park, 2) the recovery of Yellowstone area grizzly bears, and 3) big game hunting in areas surrounding the park.

The Endangered Species Act of 1973 directed the U.S. Fish and Wildlife Service (FWS) and cooperating agencies to protect and restore listed species. The gray wolf was listed as endangered in most of the contiguous 48 states. The Northern Rocky Mountain Wolf Recovery Plan, approved in 1987, offers a framework for recovery action and proposes reintroduction of wolves to Yellowstone. That proposal raised a number of questions and concerns about the potential impacts of wolf restoration.

To address some of the concerns raised, the Senate-House Interior Appropriations Conference Committee appropriated $200,000 and directed the FWS and National Park Service (NPS) to study the potential impacts of wolf restoration. The two questions addressed under this scope of work are:

1) How may a reintroduced population of wolves affect the prey base in Yellowstone National Park and big game hunting in areas surrounding the park?

2) Would a reintroduced population of wolves harm or benefit grizzly bears in the vicinity of the park?

OVERALL APPROACH TO THE PROBLEM

The NPS and the FWS selected three separate and distinct approaches to assess the effect of wolves in the greater Yellowstone area.

1) Yellowstone's Research Ecologist, Francis J. Singer, used park population counts and contacted the wildlife management agencies of the three surrounding states for their counts and hunter harvests to compile, analyze, and draft a report on the ungulate prey base for large predators in Yellowstone. The data from that draft was made available to three independent wildlife population dynamics modelers who consulted the literature and predicted the effect wolves would have on their prey in the greater Yellowstone area.

2) Interagency Grizzly Bear Study Team Leader Richard Knight and Grizzly Bear Recovery Coordinator Christopher Servheen surveyed the

North American scientific literature and predicted the effect wolves may have on the threatened Yellowstone grizzly bear population.

3) A third approach to predicting potential outcomes of complex and dynamic interactions among wolves, grizzlies, and prey species was to seek and synthesize the opinions and best judgments of experts who have studied and thought scientifically and intuitively about the interactions. Several techniques have been developed that attempt to collect and analyze the "conventional wisdom" maintained by experts in the field, while limiting some of the negative effects of group dynamics. One such method, the Delphi technique, was used in this research to assess expert opinion on the effect of wolves on Yellowstone's prey base and grizzly recovery.

THE DELPHI PROCESS

The Delphi technique consists of written questions distributed to geographically dispersed participants (Delbecq et al. 1975). Questions were answered by experts and returned to project coordinators for collation. Results were sent back to panel members for clarification, follow-up questions, and possible voting. All appendices cited in this report are available from the National Park Service, Division of Research, P.O.Box 168, Yellowstone National Park, WY.82190.

The Delphi technique is appropriate where individual judgments must be tapped and then pooled -- especially when characteristics of the task include uncertainty, inadequate data, incomplete theory, a high order of complexity, multiple objectives, and the need for intuitive and synthetic reasoning. It has been used successfully in numerous natural resource applications (Schuster et al. 1985, Miller and Cuff 1986). As such, the Delphi technique was used to identify individuals who are most knowledgeable about the interactions between wolves, grizzly bears, and prey species and then to make predictions about the future based on the collective opinions of these participants.

METHODOLOGY FOR THE YELLOWSTONE STUDY

The Delphi inquiry began in August 1989 and was completed by late December 1989. Project phases were:

1) Expert identification: August to mid-September 1989

2) First Delphi round: Mailed October 9, 1989

3) Second Delphi round: Mailed November 21, 1989

4) Review of draft document: Mailed December 28, 1989.

The Delphi uses peer referrals in development of an expert panel. A list of 25 North American wolf and prey researchers was provided by Yellowstone National

Park personnel and the FWS as a starting point. These individuals were asked to prepare a list of experts most qualified to render an opinion on wolf-prey relationships (Appendix A). From the 50 experts named, a 15-member team of most frequently mentioned scientists was assembled. All persons identified at least three times were selected. This process eliminated bias in panel selection, and assured representation by top professionals in the field. A decision was then made by the authors and Yellowstone Park staff and FWS to add several representatives with other specific types of expertise: onsite experience in Yellowstone, systems modelling from outside the wolf scientific community, and a historical long-term view of wolf research. All those identified agreed to participate. Panel members are listed at the end of this report.

After receipt of a briefing packet including a Yellowstone map and information on predator-prey relations, two Delphi mailings were initiated. Experts were asked, "Based on your experience and reading, what effects do you anticipate on prey species and grizzly bears as a result of restoration of wolves to Yellowstone?" Initial questions were based on a report by Singer, "The Ungulate Prey Base for Large Predators in Yellowstone National Park" (1989), which panelists received. Questions in the first mailing required short answers and numerical responses. The wolf-prey issues addressed included but were not limited to wolf migration, ungulate distribution and demography, prey preferences, grizzly population trends, sport hunting levels, boundary concerns, and changes over time. A copy of the first Delphi mailing and cover letter are in Appendix C. Enclosures mentioned are available through Yellowstone National Park (Greater Yellowstone Coordinating Committee 1987, Knight, et al. 1989, U.S. Fish and Wildlife Service 1987, Weaver 1978).

The second Delphi mailing was based on responses from the first round, and respondents were asked for probabilities of occurrence and levels of agreement/disagreement with the group. Findings are in Appendix D. A draft report from the study was sent to panelists and a broader circle of wolf/prey experts in late December for review and comment.

Turnaround time for each mailing was about two weeks followed by a compilation and analysis period and development of new questions. Panelist adherence to response deadlines generally was excellent, and 100% participation was achieved throughout the study, although not everyone may have answered every question.

RESULTS

Results follow, organized around the following issues: wolf numbers, wolf movements, overall ungulate impacts, species-specific impacts, effect on the grizzly bear population, sport hunting and wolf population control issues. Findings were merged from each Delphi phase. Summary statements for each question are available in Appendix E. In reporting results, "panelist agreement" refered to items where 60% or more of the panelists provided the same answer. Topics with no central convergence or a high degree of uncertainty were also identified. Most individual panelist answers and verbatim remarks are in Appendix F.

WOLF NUMBERS

The panelists were asked to estimate the number of packs that will spend the majority of their time within Yellowstone National Park after the wolf population has stabilized. There were 15 responses and a range of 3-35 packs was indicated. Seventy-three percent of the panelists predict that between 6-15 packs would spend at least 6 months within park boundaries. Using the mid-point of each estimate to calculate a mean, panelist responses averaged 13 packs.

Panelists then estimated the probability of certain specified pack levels would occur in the park. At lower pack levels (1-5, 6-10, 11-15, and 16-20 packs) there is little agreement. In fact, probability estimates in these cases range from 0% to 100%, with no central convergence. However, at higher pack levels there is more consensus that these greater population levels are less likely.

Panelists also provided a parallel estimate of the total number of wolves that would spend at least six months of the year within Yellowstone National Park. Although a total range of 24-300 wolves was indicated in the responses, slightly over half of the panelists (8 of 15) predict that between 51-150 wolves would spend at least 6 months within park boundaries. The mean population estimate was 150 wolves when calculated using the midpoint of each estimate.

Pack sizes are dynamic, varying with such factors as season, prey populations, and individual wolf personalities. When pack numbers and total population estimates made by panelists were paired, average pack size calculated ranges from 7 to 22 individuals. However, almost two-thirds (64%) of the answers calculated for mean pack size fall into the category of seven to ten individuals.

There was reason to believe that some wolves would attempt to establish territories located primarily outside of Yellowstone. When asked their opinion as to the number of packs this might represent, 67% of the responding panelists indicate between five to ten additional packs might have territories located primarily outside of the park. The most common response was five packs (six panelists), with a range of 3-20+ packs indicated by all panelists.

WOLF MOVEMENTS

Panelists generally believed that wolves have the potential to locate nearly anywhere within the park. One of the study goals was to determine potential areas for colonization by reintroduced Yellowstone wolves. A map of the park, along with reference maps of topography, average snow depth, and ungulate densities, was distributed to each panelist. Participants were instructed to mark areas of probable wolf habitation. Eleven panelists returned their marked

maps. These were then compiled into a single map representing percentage of respondents indicating probable areas of wolf colonization (Fig. 1). This information was reviewed by panelists in the second mailing.

In general, panelists felt this map was an accurate representation of potential wolf locations within the park. During the summer, wolves are expected to be found throughout the entire park. In winter, wolves would most likely be found in the north-central portion of the park. Other comments on the colonization map suggested the southeast portion of the park was overrated (i.e., not as likely to support major concentrations of wolves), the northwest area was underrated (i.e., more likely to support a greater concentration of wolves), and that there was difficulty in accurately predicting wolf locations without on-site inspection.

Because wolves would be colonizing a new area, panelists thought it would take up to 20 years to develop a stable mosaic of wolf pack territories. Territories would change in response to changing prey distribution, prey abundance, and pack size and dominance. If there was a major sustained decline in primary prey populations elk (Cervus elaphus) and mule deer (Odocoileus hemionus), there would be fewer wolves, but they would have larger territories. The opposite might hold if there is a major sustained increase in the primary prey population. Some individual pack territory boundaries might correspond to major river systems, roads, watershed divides, and other major geographic features.

In winter, wolf packs should hunt mainly in areas of low elevation where ungulates, particularly elk, aggregate. Snow depth may or may not restrict movement. Snow density, crust, and trail/road systems all play an important role when discussing limitations caused by snow. Panelists emphasized that snow depth affects ungulate movements directly and wolf movement indirectly. Packs would hunt throughout their territory with little or no use of the homesite (dens, rendezvous sites) and would be found in areas of current ungulate use within their territory. These movements would fluctuate year to year as a function of winter severity and the related major prey distribution.

A consensus can not be reached concerning when packs might leave their winter range, how often packs would visit major prey areas within their territories during winter, and whether wolves would commonly hunt in winter as a pack or periodically as a subunit of the pack.

70% or more panelists agree this area is potential wolf habitat.

40-69 % of the panelists agree this area is potential wolf habitat.

Less than 40% of the panelists agree this area is potential wolf habitat.

Fig. 1. Potential wolf habitat in Yellowstone National Park (based upon responses of 11 panelists).

In summer, panelists believed that most wolves would be within park boundaries and that wolf spatial organization should be fairly rigid, with each pack defending a home territory for rearing pups. Wolves would be most active around their homesites and would take mule deer fawns and elk, bison,(Bison bison) and moose (Alces alces) calves within the park. Wolves would make daily hunting forays from their dens and rendezvous sites, usually within the pack's territory. These forays would involve mainly subunits of the pack (one to three individuals), hunting independently and returning to rendezvous sites to feed pups and to socialize with other pack members. Panelists confirmed that it is very difficult to predict the potential location of denning sites beyond general geographic areas.In other North American locations occupied by wolves, occasional forays into neighboring pack territories have been observed. Panelists expected that such forays would also occur within the Yellowstone wolf system, but their frequency could not be predicted by a consensus of panelists. However, there was agreement that foray frequency would increase if food shortages occur. Panelists also supported the idea that packs with territories characterized by an annually variable prey base should have the greatest tendency to make extra-territorial forays in winter. Studies in other areas indicated that the frequency of forays would be important to wolf recovery because forays could cause major inter-pack hostilities and resultant wolf mortality, as well as "poaching" of prey and livestock.

Wolf dispersals refer to wolves leaving the original pack on a permanent basis. Most often singles or groups of two or three young wolves disperse. Dispersals usually are relatively localized, but sometimes entail long-distance travel hundreds of miles from the original territory.

No consensus was reached as to when wolves might disperse or how many of the released wolves might disperse. Dispersal rates may be affected by the type of initial release of reintroduced wolves. Of the wolves that disperse, panelists agreed that their chance of survival and successful colonization of new areas is uncertain. Mortality levels would be related to human-induced mortality, prey abundance, and wolf hostility. There was no agreement on whether some wolves may attempt "homing" when they are released.

GENERAL IMPACTS ON UNGULATES

Elk were expected to be the primary prey for wolves in all seasons. Mule deer also might be a primary prey during summer and a secondary prey for the rest of the year. Moose were considered potential prey, although panelists felt there was not enough data to formulate an opinion as to whether or not moose will be important prey for Yellowstone National Park wolves. Bison have the potential to be important prey depending upon a variety of factors such as type and source of wolf introduced, development of hunting skills and changing relationship with prey over time. Pronghorn (Antilocapra americana), bighorn sheep (Ovis canadensis), and mountain goats (Oreamnos americanus) would be available prey species but would not likely be important sources of food for the wolves. Further species-specific considerations are addressed in the next section.

Vulnerability

Vulnerability of prey depends on the number of individuals in a prey species, the condition of individuals, their age and sex, and the carrying capacity of their habitat. Panelists indicated that elk would be the most vulnerable prey throughout the year, except in summer when mule deer would be the most vulnerable prey. For the rest of the year, mule deer were ranked second in vulnerability. Moose, bison, pronghorn, bighorn sheep, and mountain goats were ranked progressively less vulnerable. However, because panelists stressed different aspects of vulnerability (some even using it to mean relative availability), caution is necessary when interpreting these findings.

Winter is the most vulnerable time for all prey species, with the possible exception of mule deer and pronghorn which tend to winter in areas of high human activity. Other vulnerable times mentioned were the calving seasons, rutting seasons, and in fall after a heavy snow.

Demographic Changes

Since wolves prey upon weak and inferior individuals, overall prey population condition would benefit from wolf predation. Panelists expected that wolves would select younger animals and there would be lower recruitment of young into the prey populations. Older animals also would be vulnerable to predation. Prey would be less subject to density-dependent mortality and epizootics if there were smaller fluctuations in population numbers. Specific changes in the average age of prey populations, male:female ratios, and pregnancy rates could not be agreed upon by a majority of the panelists that responded.

Regarding weather-related impacts, panelists believed that major declines in ungulate populations could occur following severe winters when prey populations were depressed. Wolf predation would reduce "pulses" in mortality now caused at intervals by very severe winters and resulting die-offs. No clear consensus among panelists could be reached on the compensatory effects of wolf predation on prey populations close to the nutrient/climate ceiling; i.e., whose numbers are being regulated by available forage and severe winter weather.

Most distribution changes of prey populations would be relatively local changes in movement, implying little geographical consequence. The primary prey would likely stay in better escape terrain, would assume more defensive behaviors, and would be more alert, skittish, and nervous.

Wolf Predation and Prey Populations

Where would wolf predation rank when compared to other factors that influence prey population levels in Yellowstone National Park? Panelists were asked to list factors in the first round of questions and to rank these factors (including wolf predation) in the second round, using the list they generated.

Three separate rankings were made for the primary prey (elk), mule deer, and the remaining ungulate secondary prey species (Table 1). Wolf predation ranked third in importance as a factor influencing elk population levels, second for mule deer, and fourth for other ungulate prey species. Forage availability as a function of weather, winter severity, and overall habitat quality were perceived to have more potential impact. Impacts on ungulates would vary over time depending on the kind of dynamic relationship that wolves and prey establish.Predation by wolves would not threaten any prey species with extinction under a 10- and 20-pack level according to 92% of the panelists; answers generally show a 0% or 1% probability of occurrence for extinction (with one dissenting panelist; see Appendix F). At a 30-pack level, deemed improbable by most of the respondents, a few panelists indicated a 5%-15% probability of extinction for any species; most answers were still 0% Several panelists remarked, "I do not believe extinction is a viable scenario."

Finally, two-thirds of the panelists did not believe a scenario with a population in excess of 300 wolves was realistic. At that level, many predicted "major" impacts on the primary (and some secondary) prey species; two panelists estimated population declines of 20%-50%. Thus the following species-specific findings focus on significantly lower pack levels.

SPECIFIC IMPACTS OF WOLF REINTRODUCTION ON PREY SPECIES

Elk

There was no consensus among panelists on changes in elk distribution following reintroduction of wolves, with the exception that calving areas may be relocated to safer areas such as slough bends, river islands, and higher elevations if these areas were in close proximity to previously used sites. Ideas that were examined included occurrence of cohesive groups, smaller aggregations, greater dispersals of individual elk, sexual segregation, migration, and relocation near man-made facilities. Sixty-six percent of the panelists (nine individuals) indicated that there would be little or moderate change in behavior and distribution among elk in Yellowstone if wolves were reintroduced.

Because many elk populations in the park are currently at high densities and show signs of nutritional stress related to competition for quality food, their numerical growth potential is limited. Therefore, wolf predation should induce an initial decline in elk numbers, which in turn would reduce nutritional stress and improve reproduction. A majority of panelists agreed that young elk likely would be preyed upon more often than adult elk in all seasons, except in winter.

Ten years after wolf reintroduction, assuming a stable wolf population of ten packs of ten wolves each, 85% of the panelists expected the elk would be reduced by less than 20%. The range of potential reductions was between 4%-30%. The most common response was a reduction of 10% (four panelists).

Table 1. Top factors that influence prey population levels in Yellowstone National Park.

Factor	Elk			Mule Deer			Other Ungulates		
	Rank	Total Frequency	Mean Score	Rank	Total Frequency	Mean Score	Rank	Total Frequency	Mean Score
Winter severity (snow depth, temp, snow conditions)	1	11	2.4	1	11	2.2	2	10	2.3
Distribution and abundance of suitable forage/general weather-vegetation interaction	2	12	2.9	3	9	3.1	1	11	2.7
Wolf predation	3	9	2.8	2	10	2.4	4	5	3.2
Habitat quality and quantity	4	7	2.9	4	8	3.6	3	9	3.0
Summer rainfall/drought	5	6	4.3	6	5	4.2	6	3	4.3
Hunting	6	8	4.9	5	7	4.3	5	4	3.8
Wildfire suppression	7	6	6.2	8	6	7.2	--	--	--
Mountain lion predation	8	7	7.9	7	7	5.6	--	--	--
Competition with livestock outside park and grazing management practices	9	6	8.0	9	5	9.0	--	--	--
Topography & drainage patterns	--	--	--	--	--	--	7	3	4.7
Bear predation	--	--	--	--	--	--	8	3	6.7
Land uses outside park that alter native habitat	--	--	--	--	--	--	9	5	7.2

Rank was determined by a two-step process:

-The ten factors were identified by the highest numbers of responses (total frequency) per factor. Thirteen panelists answered the question.

-The mean average of the panelist rankings for those factors was used to create a rank with lowest x = 1 and highest x = 10.

-- = Not top factor.

Mule Deer

As with elk, panelists provided a broad range of opinions on how mule deer behavior and distribution might change related to wolf reintroduction in Yellowstone. Areas in which panelists held a wide variety of opinions include: 1) the amount of "standing carrion", 2) relocation to water escape routes, 3) selection of hiding cover, 4) prey using territorial boundaries of wolf packs as places of refuge, or using higher elevations as refuge, and 5) moving of female/fawns closer to human habitation. Overall, however, 77% of the panelists indicated there would be moderate or little change in the behavior and distribution of the mule deer as the result of wolf reintroduction.

Mule deer ranked as the second most vulnerable species to wolf predation in fall, winter, and spring; and first most vulnerable in summer. Some panelists, however, believed that the importance of mule deer in winter was overrated due to reports indicating that mule deer on the northern range leave the park in winter and seek human-made facilities in the residential valleys nearby (e.g., Gardiner, Montana).

Panelists agreed that young mule deer would more likely be preyed upon than adult mule deer in summer and fall. The opposite should hold true during winter. Spring should see wolves preying on young and adult mule deer in approximately equal numbers.

Ten years after wolf reintroduction, assuming a stable wolf population of ten packs of ten wolves each, two-thirds of the panelists predicted a 15%-30% reduction in the mule deer population. The range of potential reductions was between 0%-30% among all panelists, with the most common response being a reduction of 20% (three panelists).

In the second scenario, three panelists predicted that reductions in mule deer numbers would vary widely (5%-50%) with 20 packs of ten wolves when compared to a system with ten packs. The most common response was a reduction of 10% (three panelists).

Bison

Panelists held widely varying opinions about the nature and extent of wolf predation on bison. The panelists were asked to describe projected wolf predation on bison and overall impacts in the region. Of 15 respondents, four predicted that wolves in Yellowstone would prey on bison only occasionally. Another five panelists indicated a strong potential for wolves to develop hunting skills over time and utilize the bison as a primary prey. The result would be more wolves wintering within park boundaries. Three panelists indicated that bison utilization by wolves is dependent upon the type of wolves introduced in Yellowstone (i.e., whether the wolves had previous experience hunting bison). Three panelists indicated that bison calves or brucellosis-

infected bison would be "training prey" for wolves inexperienced at hunting bison.

Seventy-one percent of the panelists indicated there would be little or no change in the behavior and distribution of bison related to wolf reintroduction in Yellowstone National Park.

Ten years after wolf reintroduction, assuming a stable wolf population of ten packs of ten wolves each, all panelists expected a reduction of less than 20% in the bison population is expected by all panelists. The most common response was a reduction of 10% (six panelists). With 20 packs 69% of the panelists believed the bison population would be reduced by 15% or less. Responses ranged between 0%-30%, and the most frequent responses were 10%, 15%, and 20% (three panelists each).

Moose

Sixty-seven percent of the panelists indicated there would be moderate or little change in the behavior and distribution of moose related to wolf reintroduction in Yellowstone. Most panelists felt that moose may select water escape areas (rivers, islands, lakeshores, peninsulas, etc.) for calving, avoid areas of high wolf activity, and may locate near human activity. Four panelists felt moose (with the exception of cows with calves) would not change their habits because of wolves.

Panelists agreed that moose are not highly vulnerable to wolf predation when compared with elk and mule deer. However, many panelists indicated that more information was needed on moose densities, locations, and behavior within the greater Yellowstone area before reliable predictions can be made concerning vulnerability.

Ten years after wolf reintroduction, assuming a stable wolf population of ten packs of ten wolves each, 72% of the panelists expected a reduction of 15% or less in the moose population. Responses range between 0%-30% and the most common response was a reduction of 10% (five panelists).

With moose populations under a 20-pack system, a reduction of 20% or less is expected by 77% of the panelists. Responses range between 4%-50%, and the most common response was a reduction of 10% (four panelists).

Pronghorn

Panelists agreed that pronghorn are not likely to be a primary prey for wolves in Yellowstone National Park. Eighty-six percent of the respondents (13 individuals) indicated little or no change in the behavior or distribution of

pronghorn related to wolf reintroduction in Yellowstone. The vulnerability level for pronghorn is quite low as indicated in the vulnerability ranking (Appendix F). Ninety-two percent of the panelists felt that pronghorn would be the least affected species being considered.

Reductions in pronghorn populations, under a ten-pack system ten years after wolves have been reintroduced, is expected to be less than 10% according to all panelists. Ninety-two percent of the panelists indicated a reduction of 10% or less for pronghorn populations under a 20-pack system. Total range expressed under a 20-pack system was between 0%-50%, with the most common answer being a reduction of 0% or 10% (five panelists each).

Bighorn Sheep and Mountain Goats

Panelists considered these species a secondary prey for reintroduced wolves in Yellowstone. Moderate or little change in the behavior or distribution was anticipated by 80% of the responding panelists. Panelists anticipated that bighorn sheep and mountain goats would remain in alpine areas and spend more time near cliffy escape cover. Sheep and goat vulnerability levels are considered to be quite low in comparison to the primary prey populations.

Reductions in mountain goat and bighorn sheep populations under a ten-pack system of reintroduced wolves would not be expected to exceed 5%. Under a 20}wolf pack system, a reduction of 10% or less was expected for bighorn sheep and less than 1% for mountain goats.

Beaver

Several panelists brought up the importance of small mammals, rodents, and birds in the wolf diet, focusing in particular on the beaver (Castor canadensis). Other North American wolf populations use beaver to a varying degree. Generally, panelists describe beaver as an important food source when ungulates are less available. Four panelists cited the scarcity of beaver within the park, but believed that beaver would not be heavily impacted by wolves; another four respondents thought the effect would be more significant.

Coyote

All panelists stated that the coyote (Canis latrans) population would be reduced with restoration of wolves to the Yellowstone ecosystem due to competition for food. They indicated coyote populations would shift to marginal wolf areas and peripheral areas of wolf territory. (Note: Many of the panelists probably had not seen recent research by Paquet (1989). He suggests that wolves and coyotes are sympatric where prey larger than deer are abundant.)

IMPACTS OF WOLF REINTRODUCTION ON GRIZZLY BEARS

Panelists agreed unanimously that in other locations, such as the Yukon, Alaska and Glacier National Park, wolves and grizzlies generally do well together. However, because panelists were divided about whether wolf predation would provide bears with more protein (from wolf-killed carcasses) for a greater period of the year (and a more consistent carrion supply), there was no consensus about the impact of wolf reintroduction on grizzly bears.

Four respondents described the overall effect of wolf reintroduction on grizzly bears as "slightly beneficial," four participants termed the impact "neutral," and six panelists thought the result would be "slightly negative." While there was no agreement about the direction of the impact, panelists did think the magnitude of change would be "slight" rather then "significant." The majority of the panelists who believed wolves would provide more protein (six panelists), tended to identify the overall impact on grizzlies as "slightly beneficial" (four panelists). The six panelists who thought wolves would not provide more protein called the effect "neutral" or "slightly negative." The two remaining participants who were not sure whether wolves would provide more protein took a more cautious position, describing the overall impact as "slightly negative."

The majority of panelists agreed that the omnivorous food habits of grizzly bears meant that densities of grizzly bears are not strongly linked to ungulate densities. Further, over half of the panelists (8 of 14) stated that bears do not need high ungulate populations for reproductive success if other foods are available, but bears do benefit generally from such a situation (another four panelists are uncertain).

Eleven of fourteen respondents indicated that wolves would provide some kills on which bears would feed . Bears and wolves would compete for carcasses, and occasional bear-wolf conflicts would occur at kill sites. Mortality to both bear and wolves could occur during these uncommon conflicts, but direct interspecies killing would be insignificant. Most panelists think grizzly bears would often dominate at kill sites and should be able to take over kills from wolves. In general, grizzlies would scavenge more from wolves than vice versa. There was widespread support and agreement among panelist that although there would be some predation of wolves on bear cubs and adults (females with cubs), the level of such predation would be insignificant. In total, direct wolf impacts would not be likely to produce much of an overall bear loss in Yellowstone National Park.

Similarly, other wolf-related impacts were not generally expected to occur. For example, grizzly bear activities were not expected to be restricted by the presence of wolves, even for bears that hunt ungulates in traditional calving and rutting areas. Occasional and infrequent harassment of bears by wolf packs would not be likely to reduce current bear predation opportunities. Wolves were not expected to increase the conspicuousness of ungulates by increasing mobility, with associated benefits for grizzlies. Both of the last two issues,

however, had a high degree of uncertainty associated with them (five and six panelists, respectively). There was no agreement and great uncertainty about whether wolves would occasionally dig up hibernating cubs.

Consensus could not be reached as to whether the presence of wolves would provide more food for grizzlies. Panelists could not agree on whether there would be more winter carrion and an increased number of carcasses in spring or if wolf kills would be utilized so quickly that they would not actually represent an extra food source. They also questioned whether there would be fewer opportunities for bears to scavenge on carcasses since wolves might pick them clean.

Panelists agreed further research is needed on two issues where "not sure" was the largest category of response (8 of 14 panelists for both questions). Responding to an inquiry about whether wolf kills would provide approximately 3% of grizzly ungulate foods, panelists often noted "a low percent" or "less than 5%" in their comments, but they were not willing to make an actual prediction. It also was not known whether certain segments of the bear population, most evidently breeding females with cubs, would become more alert and skittish on a regular basis.

HUNTING ISSUES

None of the panelists thought that wolf distribution should be limited to Yellowstone National Park. Eleven of 14 participants, in fact, disagreed or strongly disagreed with such a position (the others were not sure). In general, panelists argued that although the core wolf population should be centered in the park, the application of artificial or political boundaries may not sustain recovery levels. Wolves could be expected to move seasonally outside the park or to establish territories that straddle the park boundary. As such, the issue of the combined effect of hunting plus wolf predation on ungulate populations arises. Wolves would not be hunted within Yellowstone National Park.

Overall, the panel was almost evenly split over whether reduced hunting levels would be a necessary concession that came automatically with wolf reintroduction. Six respondents agreed, most of them strongly, that reduced hunting would be a necessary compromise, but some of them then mentioned that only certain species might be affected or that reductions might take place in future years rather than immediately. Seven panelists disagreed, and most of these individuals indicated that actual hunting policies would depend on the number of wolves, wolf management outside the park boundaries, and the relationship of hunted prey populations to a nutrient climate ceiling.

Panelists were then asked if they agreed that harvest levels should be reduced after wolf reintroduction. Results for each ungulate species are presented below. Figures refer to the number of panelists that gave each answer:

Response to: "Hunting levels should be reduced after wolf reintroduction..."

Species	Strongly Agree	Agree	Not sure	Disagree	Strongly Disagree
Elk	2	5	4	3	0
Mule deer	3	3	5	2	1
Bison	1	3	7	4	0
Moose	2	4	4	3	1
Pronghorn	1	0	0	9	4
Bighorn sheep	1	2	0	9	2
Mountain goat	2	0	4	7	1

There was no evident consensus or consistent opinion on a reduction in hunting activity for elk, mule deer, bison or moose -- but generally there was more agreement than disagreement. Excluding the "not sure" response, there was decidedly more support for a reduction in hunting levels for these species, with the exception of bison, where there is a split. Note that "not sure" is the largest category of response for mule deer, bison, and moose, but at most only one panelist strongly disagreed that harvest levels should be reduced for elk, mule deer, bison or moose.

Possible hunting restrictions on mule deer were characterized as "only where needed," after monitoring. For bison, expected impacts depend on whether or not they move out of the park, and panelists wanted a chance to observe how wolf-bison relationships develop over time. The lack of research and predictability about the Yellowstone moose population was mentioned, as well as the uncertainty about the actual extent of predation by wolves.

With the exceptions of a few dissenting panelists, there was more overall agreement that harvest levels will not need to be reduced for pronghorn, bighorn sheep, and mountain goats.

Participants raised related issues such as timing considerations (reductions in ungulate harvest may not be needed at first but may be necessary later), the need for research, monitoring and clear objectives prior to setting a hunting policy, and the complexity of factors that influence such a decision. A common remark was that hunting reductions could be made when and where appropriate, but blanket generalizations were not possible now. The level of hunting reductions that might be necessary was another subject where panelists held varying opinions. One panelist suggested that reductions of harvest levels to 6%-7% for all species was the only sustainable approach. Male-only hunting was also proposed under certain specified conditions.

Elk

A majority of panelists (8 of 14) disagreed that most elk herds are hunted near maximum sustained yield, and mention that it varies by herd. Most herds were

thought to be harvested near or below sustained yield; some lightly exploited populations are increasing. Because of very high current elk densities in and near the park, thinning of the elk herd was described as desirable. Ten respondents (67%) agreed that the sustainable elk harvest would decline with elk predation, but the same number thought that even at a 20-pack level, sport hunting would still be possible. There was no agreement on the level of annual elk harvest or if male-only elk hunting would be recommended if wolves were reintroduced.

Mule deer

Most panelists (10 of 14) agreed that where mule deer harvest levels currently exceed 20%, the impact of wolf predation could be severe. However, half of the respondents (six individuals) believe hunting would be possible even with a population of 100 wolves; another five experts were not sure. Similar to the response for elk, there was no consensus about the level of mule deer harvest that would be sustainable or if male-only hunting would be needed.

Bison

The bison hunting level has been generally low, except during the winter of 1988-1989 when bison moved outside the park and hunters harvested 568 animals. Most bison usually stay in the park; but if they did move out, there would be potential for a significant impact as a result of successful wolf predation and high levels of hunting. Ten of 14 panelists agreed that the impact of hunting plus wolf predation would depend on whether bison were preferred by wolves, and that the pattern of bison utilization by wolves could not be predicted. In this uncertain situation, panelists generally supported (with two dissentions) no changes in bison harvest levels at the present time, stating that because bison are easily counted and harvest is tightly regulated, human harvest could be quickly eliminated if the population were severely impacted.

Moose

The moose hunting issue was clouded because of a lack of information about the population in the Yellowstone area. For example, 10 of 14 panelists said they were not sure if most moose in the park are year-round residents. At high moose harvest levels of between 10%-20%, panelists said wolf predation could have a "severe" impact on moose populations.

HUNTING AND WOLF PREDATION

All thirteen panelists answering agreed (five "strongly agree") that it could not be assumed that a reduction in hunting would simply make up for wolf kills in an additive manner. This concept is key to managing a system where sport hunting is a factor, since hunting and predation do not kill the same animals.

Hunting takes adults; predation, on the other hand, concentrates on the young and old. Both elements, however, are highly selective and density-dependent.

Some of the ungulate species could eventually see severe declines with wolf predation if human harvesting was high, especially if this coincides with a run of severe winters (8 of 13 panelists agree). It would be difficult to accurately distinguish population changes strictly due to predation by wolves.

HUNTING AND WOLF CONTROL

Interaction in a multiple-prey system is made more complex by the inclusion of sport hunting. Panelists were unanimous in their opinion that hunting and wolf control must be addressed integrated factors, rather than an either/or approach. They totally rejected the position that effects on ungulate populations could be managed either by reducing predation by lowering wolf numbers outside the park or reducing hunting (but not both). However, beyond the agreement that problem wolves which kill livestock must be removed, there was no agreement about the combination of management strategies that would best meet multiple objectives.

The majority of panelists agreed that the objective outside the park should be wolf population control (by the most effective means) not eradication. Those that disagreed generally perceived population control as a periodic solution, and supported comprehensive ongoing management strategies rather than a simple reduction in wolf numbers. Respondents were split on whether wolf control measures should start immediately upon introduction. Some believed wolf control would be a political necessity to get the program started, while others believed there was not enough data to make decisions or that control measures may need to change over time (e.g.) relocation in early phases, elimination of problem wolves in later stages) and could not be prescribed immediately.

Finally, the panelists did not accept establishing a minimum population size for each prey species and initiating wolf control measures only if these population levels are reached. Their reasons were lack of information and concerns about "crisis management."

CONCLUSIONS

Overall, the following main points emerged from panelist deliberations:

Panelists unanimously agreed that wolves were part of the original ecosystem in Yellowstone National Park.

The core wolf population should be centered in Yellowstone National Park, but the application of artificial or political boundaries may not sustain recovery levels.

A viable wolf population of about a dozen wolf packs that spend the majority of their time within the park seemed realistic after the population had stabilized (within 20 years after reintroduction).

If wolves were reintroduced, extinction of any prey species (elk, mule deer, moose, bison, pronghorn, bighorn sheep, and mountain goat) was thought to be extremely unlikely.

There would be relatively minor changes in prey species' behavior and distribution if wolves were reintroduced in the park.

Elk and mule deer would be the primary prey for wolves -- elk throughout the year, mule deer in summer. Other prey species would be relatively minor sources of food.

Panelists agreed unanimously that wolves and grizzly bears could coexist. However, there were differing opinions about specific impacts of wolf reintroduction on grizzly bears, in particular with regard to whether wolf predation would provide bears with more protein from wolf-killed carcasses and a more consistent carrion supply. All panelists called the overall impact "slight" or "neutral."

Reduced big game hunting levels would not be an automatic requirement if wolves were restored to the Yellowstone ecosystem. Reduced hunting levels should be implemented only when necessary, and then only in conjunction with wolf control measures and other prey population management tools.

More research is needed to better understand the interrelations among wolves, grizzly bears, prey species, and big game hunting in areas surrounding the park.

It is important to emphasize that the Delphi does not try to achieve panelist consensus. No ideas introduced into the process are lost (Appendix F), and "minority opinions" are actually a rich source of ideas for further study, discussion, and analysis. It is hoped that the information complied through this process will provide a starting point for further dialogue. The Delphi technique assumes equal expertise by all participants on all issues, an assumption that can not be met for the Yellowstone wolf study. As such, the Delphi is often used in combination with group interaction to sharpen panelist responses and provide an opportunity to discuss specific subject matter in greater detail. This report represents a first step toward understanding the complexity of wolf-prey interrelationships and offers an overview by 15 experts on the significant issues.

Delphi Panel Members

Dr. Durward Allen
Dept. of Forestry &
Natural Resources
Purdue University
West Lafayette, Indiana 47907

Warren Ballard
Alaska Dept. of Fish & Game
P.O. Box 1148
Nome, Alaska 99762

Dr. A. T. Bergerud
Dept. of Biology
P.O. Box 1700
Victoria, British Columbia
Canada V8W 2Y2

Dr. Ludwig N. Carbyn
Canadian Wildlife Service
4999 - 98 Avenue
Edmonton, Alberta
Canada T6B 2X3

Dr. William C. Gasaway
Alaska Dept. of Fish & Game
Div. of Wildlife Conserv.
1300 College Road
Fairbanks, Alaska 99701

Dr. Gordon Haber
Wildlife Scientist
P.O. Box 64
Denali National Park, Alaska 99755

Dr. David L. Mech
Wildlife Research Biologist
U.S. Fish & Wildlife Service
c/o North Central Forest Experiment Station
1992 Folwell Avenue
St. Paul, Minnesota 55108

Dr. Francois Messier
Dept. of Biology
University of Saskatchewan
Saskatoon, Saskatchewan
Canada S7N 0W0

Dr. James M. Peek
Dept. of Fish &
Wildlife Resources
University of Idaho
Moscow, Idaho 83843

Dr. Rolf O. Peterson
School of Forestry &
Wood Products
Michigan Technological University
Houghton, Michigan 49931

Dr. Robert R. Ream
Wolf Ecology Project
School of Forestry
University of Montana
Missoula, Montana 59801

Dr. John B. Theberge
Faculty of Environmental Studies
University of Waterloo
Waterloo, Ontario
Canada N2L 3G1

Dr. Victor Van Ballenberghe
U.S. Forest Service
Institute of Northern Forestry
201 East 9th Ave., Suite 206
Anchorage, Alaska 99501

John Weaver
University of Montana
Former National Grizzly Bear
Habitat Coordinator, USFS
P.O. Box 8594
Missoula, Montana 59807

Dr. Carl Walters
Dept. of Zoology
6270 University Blvd.
University of British Columbia
Vancouver, British Columbia
Canada V6T 2A9

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SECTION 5

Proposed Studies for 1990

PROPOSED STUDIES FOR 1990

John D. Varley, National Park Service, Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190

Recognizing that a number of concerns remain, these topics will be investigated in 1990:

- How vulnerable might moose on the northern range be to reduction by combined human harvest and wolf predation?
- Elk calf mortality - what kills the calves and when?
- How will wolves affect the Jackson Hole elk herd? (computer modeling)
- How can DNA fingerprinting help us positively separate wolves, coyotes, and domestic dogs, and characterize how closely wolves and coyotes of Yellowstone are related to others in the northern Rocky Mountains?
- What does the paleontological and archeological literature tell us about wolf prehistory in the greater Yellowstone area?
- What can a sophisticated computer model tell us about mule deer and elk population dynamics in greater Yellowstone?
- What effects will the 1988 fires and winter range acquisition have on wolf/elk predictions? (computer modeling)
- How will wolves and grizzly bears affect each other in the Firehole River area, where bison as carrion are seen as critical to grizzly bear welfare?
- What is the small mammal prey base for wolves, and what percentage of a wolf's diet might consist of small mammals in Yellowstone?
- How will wolf recovery affect the region in social and economic terms?

Numerous other questions may be addressed by future studies.

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REVIEWERS

Draft portions of this document were sent to the following individuals for their comments and review.

National Park Service
Norman Bishop
Wayne Brewster
Douglas Houston
Dan Huff
Dick Knight
Mary Meagher
Michael Ruggiero
Rich Klukas
John Varley
Susan Mills
Francis Singer
Stu Coleman
Paul Schullery
John Mack
Sue Consolo

U.S. Fish and Wildlife Service
Steve Fritts
Kemper McMaster
Chuck Lobdell
Jay Gore

U.S. Forest Service
Kirk Horn

Universities
Lee Metzgar, University of Montana
Mark Boyce, University of Wyoming
Dave Vales, University of Idaho
James Peek, University of Idaho

State Fish and Game Departments
Ruth Gale, Idaho
Jim Yorgason, Wyoming
Garvis Roby, Wyoming
Kurt Alt, Montana
Tom Lemke, Montana

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James Peek, University of Idaho

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Tom Lemke, Montana

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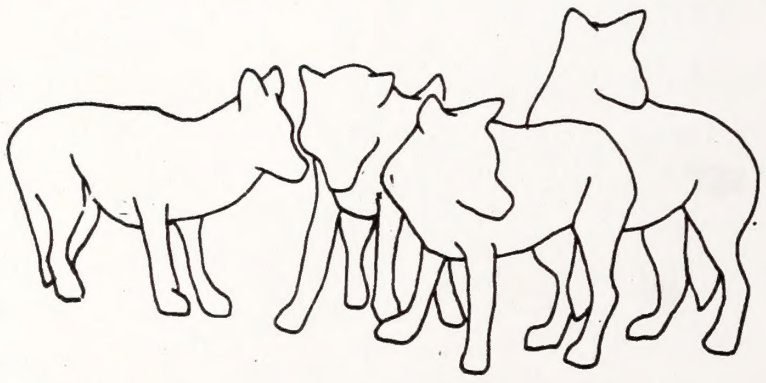
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